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The taxonomy of Lotus corniculatus L. sensu lato

by

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A Thesis submitted to the University of Glasgow for
the degree of Master of Science.

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2.

Abstract

Plant material corresponding to L. corniculatus s.l. was collected from a number of sites in the British Isles, continental Europe, North America and New Zealand, and grown in experimental plots. Various morphological features were examined and the plants identified as L. corniculatus s.s., L. uliginosus and L. tenuis according to published descriptions. Two forms of L. corniculatus were recognised; those with all stems decumbent and those with any or all stems ascending or erect.

The range of variability in the characters most frequently used for identification was determined. The standard deviation of these characters for each population was compared. A number of characters : hairiness, shape and length of calyx teeth, stem length, leaflet shape, and leaflet epidermal cells showed a wide range of variation and considerable overlap between species. However, the characters of appearance of calyx teeth in bud, presence of rhizomes, seed length and number of flowers per inflorescence showed some discontinuity, proving of most value for discriminating between species. Other characters: hollowness of stems, prominence of leaf veins and leaflet length: breadth ratio were found to be indicative of species but were not consistently reliable.

Transplantation of plants from various wild habitats into more or less uniform conditions showed that under cultivation significant changes take place in leaflet length and leaflet length:breadth ratio.

Morphological differences between the two forms of L. corniculatus were often found to be greater than between the erect form of L. corniculatus and L. uliginosus. In some cases difficulty was experienced in distinguishing these two species in the field. Chromosome counts confirmed the number of chromosomes in L. corniculatus as 24 and in L. tenuis and L. uliginosus as 12.

It is proposed that sufficient distinction exists between the two forms of L. corniculatus in Britain to warrant their having sub-species status. It is suggested that appropriate nomenclature for the erect form is sub-species vulgaris Koch and the decumbent form sub-species arvensis Pers., following work by MacDonald (1946). The descriptions are as follows:

L. corniculatus L. ssp vulgaris Koch

Plants varying in form from having some, but not all, stems decumbent to ascending or erect. Stems (2) 25-50 (60) cm, usually solid at base but frequently becoming hollow. Internodes long 15-38cm. Peduncles (2) 3-10 (13) cm. Leaves glabrous or hairy, ovate or obovate often mucronate, 8-21mm long, usually more than twice as long as wide, veins usually absent or scarcely apparent. Inflorescence 3-8 flowered. Calyx teeth erect in bud. Underground stems absent. ($2n = 24$).

L. corniculatus L. ssp arvensis Pers.

Plants with all stems decumbent, low and spreading. Stems (5) 10-25 (35) cm, usually solid. Internodes short 5-13cm. Peduncles erect (1) 2-7 (9) cm. Leaves glabrous or hairy, ovate or obovate (3) 5-12 (15) mm long, usually less than half as long as

wide, veins usually absent. Inflorescence 1-6 flowered. Calyx teeth erect in bud. Root stock short and thick, often woody with underground stems. ($2n = 24$).

Existing cultivars have been identified as the erect form of L. corniculatus. They show much morphological similarity with no ability to propagate themselves by rhizomatous growth. A range of unexploited sources of genetic material exists which could be used for the establishment of a breeding programme to improve the agronomic potential of indigenous L. corniculatus.

3.

Introduction

The aggregate species Lotus corniculatus L. is one of much variability, and while it is generally agreed that it includes L. corniculatus L. sensu stricto, L. uliginosus Schkuhr and L. tenuis Waldst. & Kit., taxonomists over the years have disputed nomenclature, the existence of sub-species and varieties, and the status of several forms of limited geographical distribution.

One of the aims of this work has been to study the history of the taxonomy of the species in order to assess the basis for some of the differences which exist in modern classifications. As much as possible of the range of variation within the aggregate species has been investigated in order to establish the validity of these classifications.

Birdsfoot trefoils of this group of species are native to Europe, temperate Asia and North Africa as far south as Ethiopia (Zeven & De Wet, 1982) but they have since been introduced into most other temperate zone countries of the world because of their potential for forage production. They are capable of outyielding other temperate forage legumes such as lucerne and red and white clovers (Hoveland, Haaland, Harris & McGuire, 1982). Moreover, they are tolerant of soil acidity and drought and do not cause problems of oestrogen content and bloat.

Birdsfoot trefoils have not become widely used in agricultural practice because of poor seedling vigour, slow establishment, failure to persist after cutting or grazing and low seed yields resulting from indeterminate flowering and pod shattering.

A further aspect of the investigation has therefore

been to consider whether any of the characters which may be found within the species, but are not at present found in commercial cultivars, could be incorporated in order to improve its agromomic value.

4.

The History of the Taxonomy

L. corniculatus sensu lato is a group of species showing a considerable range of phenotypic variation. Through time this has allowed taxonomists to select and describe many different characters. Opinions on how the group should be divided have changed as awareness of the extent and nature of the variation has grown. Uncertainty about the diagnostic value of much of this variation has allowed a number of different classifications to emerge. It is now apparent that accurate identification of some members of this group is extremely difficult.

Even the origin of the generic name, "Lotus" is uncertain. Gray (1821) traces it to Theophrastus (370-285 B.C.) and the very beginnings of plant morphology. Withering (1830) was less certain and stated that the origin of the name seemed involved in mystery, possibly being of Egyptian extraction and derived from the Greek "Io", meaning, "to desire". A more prosaic explanation has been offered by Brimble (1949). He stated that a more likely origin was from the Greek 'lotos' meaning trefoil and that there are no associations with the lotus made famous by the lotus-eaters of Homer's Odyssey.

A species of Lotus was certainly growing in Britain in the 17th Century. Gerard (1633) describes in 'The Herbal or General History of Plants' a "horned Clauer" or "codded Trefoile"™ which he translates into Latin as Lotus trifolia corniculata.

"The horned Clauer, or codded Trefoile, groweth up with many weake and slender stalks lying upon the ground: about which are set white leaves, somewhat long, lesser, and narrower than any of the

other Trefoiles: the floures grow at the tops, of the fashion of those of Pea but of a shining yellow colour: after which come certain straight cods, bigger than those of Fenegreeke but blunter at their ends, in which are contained little round seed; the root is hard and wooden and sendeth forth young springs every year."

The accompanying plate (Plate 1) indicates a more robust plant than expected from the description with broad pods and few flowers per inflorescence.



Plate 1:

Although a number of unusual features are apparent, such as the absence of two opposite leaflets at the base of the petiole, this plant may well be thought of as the plant described by Linnaeus as Lotus corniculatus.

Linnaeus published his classification in *Species Plantarum* (1753). He recognised 15 species including Lotus rectus, L. hirsutus, L. tenuifolius as well as L. corniculatus. Although his diagnostic phrases are vague and at times ambiguous (Linnaeus held that his diagnoses should not exceed 12 words (Stern, 1973))

they provide the basis of subsequent classifications.

Lotus hirsutus

- "11. *LOTUS capitulis hirsutis, caule erecto hirsuto, leguminibus ovatis. Hort. ups. 220. Sauv. monsp. 188.*
Lotus caule fruticosa, florum capitulis depressis, calycibus lanigeris. Hort. cliff. 372. Roy. lugdb. 387.
Lotus pentaphyllos siliquosus villosus. Bauh. pin. 372.
Lotus polyceratos frutescens incana alba, siliquis erectis crassioribus & brevioribus rectis. Moris. hist. 2. p. 177. s. 2. t. 18. f. 14.
Habitat in G. Narbonensi, Italia."

"Lotus with hairy heads, upright hairy stem, pods ovate.

Lotus with bushy stem, the flowers are in heads and flattened from above, woolly calyx.

Lotus with five leaves, hairy pods.

Lotus many podded, becoming shrubby white dull white, pods upright, thicker and shorter, straight."

Lotus rectus

- "12. *LOTUS capitulis subglobosis, caule erecto, leguminibus rectis glabris. Hort. ups. 221.*
Lotus caule fruticoso, florum capitulis globosis. Hort. cliff. 372. Roy. lugdb. 387. Sauv. monsp. 188.
Lotus siliquosus glaber, flore rotundo. Bauh. pin. 332.
Lotus polyceratos frutescens hirsuta alba major latifolia, siliquis tenuibus curtis rectis. Moris. Hist. 2. p. 177. s. 2. t. 18. s. 13.
Habitat in G. Narbonensi, Sicilia, Calabria."

"Lotus with almost spherical heads, upright stems, straight glabrous pods.

Lotus with bushy stem, the heads of the flowers spherical.

Lotus glabrous, podded, flowers rounded.

Lotus many podded becoming shrubby, hairy, white, greater, broad-leaved, pods slender short and straight."

Lotus corniculatus

- "3. LOTUS capitulis depressis, caulibus decumbentibus leguminibus cylindricis.
Lotus caule herbaceo, florum capitulo depresso, leguminibus decumbentibus teretibus. Hort. cliff. 372. Fl. sus 609. Roy. lugdb. 388. Dalib. paris. 221.
Lotus f. Melilotus pentaphyllos minor glabra. Bauh. pin. 332.
Trifolium corniculatum. Dod. pempt. 573.
β Lotus pentaphyllos, flore majore luteo splendente. Bauh. pin. 222.
γ Lotus pentaphyllos frutescens, tenuissimis glabris foliis. Bauh. pin. 332.
Trifolium corniculatum frutescens, tenuissimis foliis. Bauh. prodr. 144. Burs. XVIII. 73.
Habitat in Europa.
Hujus forte varietas etiam γ. est, cujus Caules duple longiores & angustiores, Folia linearia, & Legumina angustiora. Videtur in umbra nata; Burserus C. Bauhino hanc attulit."

"Lotus with heads flattened from above, decumbent stems, cylindrical pods.

Lotus with slightly fleshy stems, heads of flowers flattened from above, pods decumbent and tapering.

Lotus or Melilotus five-leaved, smaller, glabrous
Trifolium corniculatus.

β Lotus five-leaved, larger flower brilliant yellow.

Lotus tenuifolius

γ Lotus five-leaved becoming bushy, very slender glabrous leaves."

This description of Lotus tenuifolius is in fact an earlier description taken from Bauhin's (1623) synonymy of plant names

'Pinax Theatri Botanici'. Linnaeus states that:

"perhaps L. corniculatus γ (L. tenuifolius) is a variety of this [Lotus corniculatus], the stems being twice as long and narrow, the leaves linear and the pods narrower. Arising in shady places, Burser brought these [facts] to the attention of C. Bauhin."

It is apparent from these diagnoses that L. corniculatus is a decumbent plant bearing decumbent pods, with L. tenuifolius being a more narrow-leaved and slender-stemmed form. L. hirsutus and L. rectus, however, are both upright plants, L. hirsutus being distinguished by its hairiness and L. rectus by its spherical inflorescence and straight or horizontal pods.

In 1772, Scopoli published his observations of the group in 'Flora Carniolica' and mentions two species; L. corniculatus and L. major.

His initial description of L. corniculatus is the same as that of Linnaeus.

"LOTUS corniculatus.

*Lotus capitulis depressis; caulibus
decumbentibus; leguminibus cylindricis,
patentibus. LINN. Syst. Nat. p. 505.
Spec. Plant. p. 775. n. 13. Fl.
Succ. 2. 675. Fl. Carniol. p. 535. n. 1.
Lotus floribus umbellatis; siliquis pendulis;
caule procumbente. HALL. Enum. p. 572. n. 3.
Habitat in pratis et collibus herbidis;
initio M. Maii florens.
Caulis sola basis, apud nos procumbens.
Umbella 4-5-flora. Calycini dentes villosuli.
Filamenta omnia apice dilatata. Stigma
incrassatum, ovale, acuminatum. Siliqua
uncialis, recta, nitens, fusco-rubra, arido
stylo terminata."*

"Lotus with heads flattened from above, decumbent stems, cylindrical spreading pods. Linnaeus.

Lotus with umbellate flowers, pendulous pods, procumbent stem.
von Haller.

Habitat: It grows in meadows and on grassy hills; flowering from the beginning of May.

The bases of the stems lie on the soil, procumbent in our area (according to us). Umbels of 4 to 5 flowers. Calyx teeth slightly hairy. All filaments dilated at tip. Stigma thickened, oval, acuminate. The pods one inch long, straight, glossy, dark reddish-brown terminating in a withered style."

Why Scopoli includes the earlier (1742) description of L. corniculatus by von Haller, one of Linnaeus's foreign correspondents, is not clear. His version appears to be not at all like L. corniculatus, but more like a procumbent form of L. major with the same pendulous pods.

Scopoli later in his account elaborates on the question of the pods, contradicting von Haller by describing them as straight (or upright) but not pendulous.

The description of L. major is as follows:

"*LOTUS major.*

Lotus floribus umbellatis; siliquis pendulis;

caule erecto. HALL. Enum. p. 571. n. 2.

Loti corniculati major species. I. BAUH.

Hist. II. p. 355.

Habitat iuxta vias in siccis; sub finem M.

Maii florens."

"Lotus with umbellate flowers, pendulous pods; upright stem. von Haller.

Lotus corniculatus major species. Bauhin.

Habitat: Commonly found beside roads in dry areas. Flowers before the end of May."

This upright plant, with pendulous pods, inhabiting dry areas, would appear to be an upright form of L. corniculatus, not described by Linnaeus. There is no evidence to suggest a link between this plant, L. major, and L. rectus, for Linnaeus fits

Bauhin's description "*Lotus siliquosus glaber, flore rotundo*" to L. rectus, whereas Scopoli uses Bauhin's description "*Loti corniculati major species*" for L. major.

There is also a clear difference in the attitude of the pods which are straight in L. rectus L. and pendulous, according to von Haller in L. major. Scopoli makes no mention of the more slender form, L. tenuifolius described by Linnaeus.

Schkuhr's (1796) classification in 'Botanisches Handbuch' provides much more information on the genus and describes four species of interest; L. rectus, L. hirsutus, L. uliginosus and L. arvensis.

He states of L. rectus;

"*Lot. rectus. Gerader Schotenklee; mit fast tugelrunden Blumenköpfen, einem geraden ebenen Stamme, und geraden, glatten hülsen. Wächst in Sicilien und Calabrien wild, und ist in Gärten Dlds. strauchartig. Die Stämme sind im hiesigen botan. Gärten ungefähr. 2' oder drüber hoch, und sammt den Zweigen, Blättern, Blattstielen und Kelchen haarig. Die dreifachen Blättchen sind stumpf enrund, oder fast keilformig, und endigen sich mit einer kleinen spisse. Die Blumen sind gelb, die Zähne des Kelchs ziemlich gleich, und die Narbe ist kopfförmig. Bl. im Jul.*"

"Upright horned clover"

Plants with almost round flower heads, upright, smooth stems and straight glabrous pods. It grows wild in Sicily and Calabria and is found as a bushy species in German (botanic) gardens. In gardens the stems are 2 feet or more tall, with stems, leaves, pedicels and sepals more or less hairy. The tripartite leaves are rounded, becoming wedge-shaped or end in a small point. The flowers are yellow. The calyx teeth are of equal length and the stigma is head-shaped."

This fuller description of L. rectus contains phrases used by Linnaeus in his diagnosis, so there can be some certainty that the same plant is being described, although according to Schkuhr it is a plant with a limited distribution.

Schkuhr's description of L. hirsutus similarly follows the Linnaean model and is a plant with a much wider distribution.

"Lot. hirsutus. Zottiger Schotenklee; mit fast runden Blumenköpfen einem aufrechten steifhaarigen Stamme, und enrunden Hülsen. Wächst ausser Frankreich, Italien und der Levante, auch in Bayern wild, und ist auch in deutschen Gärten $\frac{1}{2}$, oder $\frac{1}{3}$. Die Blattchen sind langlich, an beyden Enden zugespitzt, und stehen zu 4-5 auf ihrem Stiel. Die Kelche sind wollig; das Fähnchen ist blassgelb, die Flügel weisslich, und das Schiffchen an der Spitze schwarz. Bl. in Sommer."

"Hairy horned clover"

Plants with almost round flower heads and upright stem with stiff hairs and oval pods. It is perennial growing in France, Italy and the Levant and also wild in Bavaria and is also in German (botanic) gardens. The leaves are longish, pointed at both ends with 4 or 5 to a stem.

The calyx is hairy and the standard petal pale yellow, the wings whitish and the keel is black at the tip."

In what appears to be the first account of L. uliginosus Schkuhr states;

"Lot. uliginosus Sumpf Schotenklee, Sumpf Hornklee, gehörnter Sumpfklee; mit runden rohrigen Stängeln und Blumenstielen k, gefranzten zurückgekrumnten kelchspissen a, und walzenförmigen, abstehenden Hülsen c. Diese und folgende Art stehen nach Linné und ubrigen mir bekannten Schriftstellern als Ubänderungen unter L. corniculatus, in ganz Did. $\frac{1}{2}$, die ich aber, nach vielfaltigen Beobachtungen, für zwey ganz verschiedene Arten halte, und den angegebenen Unterschied für beständig gefunden

habe; ungeachtet sie sich auch nach in andern Stücken unter Scheiden, wovon die jessige Art gewöhnlich aus feuchten, nassen oder sumpfigen schattigen Wiesen und andern ähnlichen Orten wächst. Die Stängel sind 1', 2' und drüber lang, aufgerichtet, sammt den Zweigen und Blumenstielen rund und hohl. Die Zähne des Kelchs sind; besonders vor dem Aufblühen der Blume, rückwärts gebogen und ausgebreitet. Die Hülsen sind allezeit länger als folgende; die Saamen kleiner, ausserlich gelblichbraun und inwendig gelb. Bl vom Jun. bis Aug. Bitternb. im Stadtgraben und andern Orten.

"Marsh horned clover

Plants with round, hollow stems and peduncles. The calyx teeth are bent back and the pods upright. This and the following types are according to Linnaeus and other writers known to me, variations on L. corniculatus, but after much observation I consider L. corniculatus to be quite different from L. uliginosus. L. uliginosus grows in marshy, shady meadows and other such places. The stems are 1 foot, 2 feet tall or even taller and the stems and peduncles are rounded. Particularly before the flower opens the calyx teeth are bent backwards and spreading. The legumes are longer, the seeds smaller, yellowish brown on outside and yellow on the inside."

This description of L. uliginosus as a wetland species with hollow stems, upright pods and with calyx teeth spreading in bud distinguishes it from any previously described species. Schkuhr contrasts it with the following species, L. arvensis.

"Lotus arvensis. feld=Schotenklee, kleiner hornklee, gelbe Vogelwicke, kleiner gelber honigklee, güldnerklee, wilder Steinklee, frauenfingerkraut; mit eckigem Stängel und nicht röhrigen Blumenstielen, ausrechten Kelchsähnen, und waltzenformigen, abstehenden Hülsen. Wächst in ganz Did. auf trocken Wiesen, an Wegen und Ackerreinen h. Die Stängel sind gestreckt, ungefähr eine Hand und drüber lang; bis weilen scheinen die Blättchen mehr stumpf, als bey vorigen. Die Blumen sind gelb, vordem Aufblühen

oft röthlich, und die Kelchzähne zusammengezogen. Die Hülsen sind kürzer als bey der vorigen Art, die Saamen grosser, äusserlich braun und inwendig grün. Bon beyden sind die Hülsen geoffnet, und ein Same; vergrössert durchschnitten. Bl. mit vorigem. Wittb. auf dem Wall und andern Orten. Ist frisch und trocken ein gutes Futter; die Blumen für die Bienen.

"Field, small, yellow, small yellow or wild horned clover

Plants with angular and not hollow stems. Upright calyx teeth and upright legumes. It grows all over Germany in dry meadows and paths. The stems are procumbent, about a hand or even longer. Sometimes the leaves are more rounded than L. uliginosus. The flowers are yellow, often tinged with red before opening and the calyx teeth are tight together. The pods are shorter than previously and the seeds bigger, brown on outside and inwardly green."

Although L. arvensis appears to be the type of small, decumbent plant thought of by Linnaeus as L. corniculatus, there is an apparent difference of opinion about the appearance of the pods. Schkuhr describes the pods as being straight or upright, whereas Linnaeus claims them to be decumbent and cylindrical, and Scopoli to be spreading and cylindrical or straight. Possibly this is not the inconsistent character it appears to be, but a matter of different use of terminology. 'Spreading', 'straight' and 'decumbent' may all take the meaning, 'horizontal to the ground'.

Von Haller is the only author to describe the pods as pendulous. This observation he applies not only to decumbent forms but also to upright forms of L. corniculatus with which L. major and subsequently L. rectus and L. uliginosus are later associated. In the case of the latter two named species the pods are indisputably not pendulous.

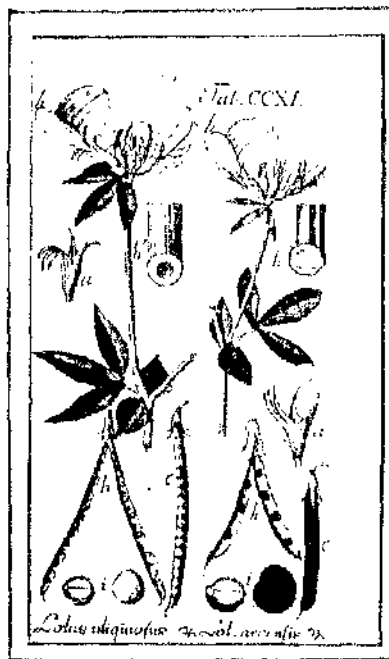


Plate 2:

This plate (Plate 2) from Schkuhr's "Botanisches Handbuch" illustrates various characters which distinguish L. uliginosus from the more decumbent forms of L. corniculatus. L. uliginosus can be seen to have a larger number of flowers per head, reflexed or spreading, villous calyx teeth, a hollow stem and longer, narrower pods containing smaller seeds than L. arvensis.

Three years previously in 1793, Cavanilles had published in 'Icones et Descriptiones Plantarum' a description of a plant possibly similar to L. major Scopoli, named L. pedunculatus. Cavanilles states:

"LOTUS PEDUNCULATUS

*LOTUS caule herbaceo: foliolis lanceolatis, medio
petiolato: floribus longe pedunculatis.
Caulis herbaceus, teres, tripedalis, glaberrimus ut
et tota planta.
Folia lanceolata, apice acuta, non ita ternata, ut
tria foliola in apice sedeant petioli communis;*

*sed quemmadmodum in melilotis gaudeat proprio
petiolo ad cuius basim sedent reliqua: stipulae
ovato-acuminatae, foliis latiores et breviores.
Flores umbellato-capitati, sustentati pedunculo
axillari, solitario, fere semipedali: in huius
apice folium ternatum sessile absque stipulis
existit, quod involucris vices gerit.
Calix turbinatus, oblongus, semiquinquepartitus,
laciniis subulatis, subaequalibus.
Corolla papilionacea lutea: vexillum ovatum alis
paulo longius: istae sunt oblongae basique
lunatae: carina brevior, basi bisetosa.
Genitalia ut in congeneribus.
Fructus deerat.
Habitat copiose iuxta oppidum Mentrída in tractu
vulgo Arroya de Valdegótera. Floret Iulio."*

"Lotus with green fleshy stem: lanceolate leaflets, with the middle petiolate: the flowers with elongated peduncles. The stem is fleshy, tapering upwards, 3 feet long, very glabrous, as is the whole plant.

Lanceolate leaves with pointed tips, not in threes, so that three leaflets share a common petiole, but the middle leaflet has its own petiole at the base of which are found the remnants: ovate stipules, coming to a point, broader and shorter than the leaves.

Flowers with umbellate heads, supported by axillary peduncles, single, nearly half a foot long: at the tip there is a sessile tri-partite leaf.

Calyx obconical, oblong, divided halfway into 5 parts, awl shaped almost uniform in length.

Yellow pea-like corolla, standard ovate, longer at wings, these are oblong and crescent shaped at base; shorter keel with 2 bristles at base.

Stamens and pistils the same as other members of the genus.

Fruit lacking (when examined).

Habitat - plentiful around the town of Mentrída on land commonly known as Arroya de Valdegótera. Flowers in July."

The following Plate (Plate 3) is taken from 'Icones et Descriptiones Plantarum' by Cavanilles (1793). It illustrates an upright plant with straight calyx teeth and glabrous, fleshy stem.

LOTUS PEDUNCULATUS.



A.J. Cavanilles del.

M. Gamberino Sculp.

Explic. tab. a Flos integer. b Calix. c Petala expansa. d Germen. e Stamina.

It is apparent that L. pedunculatus Cav. more closely resembles L. major Scop. or L. rectus L., than it does L. uliginosus Schk. The differences between the calyx teeth of L. pedunculatus and L. uliginosus are distinguishable as is the contrast in the fleshiness of the stem.

Unfortunately, no description of the pods of L. pedunculatus was made by Cavanilles so that whether the pods were pendulous, as of von Haller's description of L. major or straight and spreading as of L. rectus remains uncertain.

A summary of the situation at the end of the 18th century is represented in Table 1.

In 1809 Willdenow published 'Enumeratio Plantarum Horti' in which he retained the Linnaean diagnosis for the genus Lotus with the exception of L. tenuis. This he regarded as a distinct species and not a variety of L. corniculatus. Using the original diagnosis of Waldstein and Kitaibel from 'Descriptiones et Icones Plantarum' (1799-1812) he states:

"LOTUS tenuis.

*L. leguminibus subquaternis teretibus aristatis,
caule decumbente ramoso, foliolis lineari-
lanceolatis glabris.*

Lotus tenuis. Waldstein et Kitaibel.

Habitat in Hungaria. L. D."

"Lotus with no more than 4 aristate tapering pods, branching, decumbent stem, linear-lanceolate leaflets - glabrous.
Habitat in Hungary."

This description becomes the reference point for many later botanists.

Major changes were brought about by de Candolle who published his revision in 'Prodromus Systematis Naturalis' between

Author	Date Publ- ished	Equivalent Species					
		Lotus siliquosus glaber, flore rotundo	Lotus pentaphyllos siliquosus villosus	Melilotus pentaphyllos minor glabra	Lotus pentaphyllos frutescens tenuissimis foliis	Lotus corniculatus major species	
Bauhin	1623						
von Haller	1744			Lotus floribus umbellatis; siliquis pendulis; caule procumbente		Lotus floribus umbellatis; siliquis pendulis; caule erecto	
Linnaeus	1756	Lotus rectus	Lotus hirsutus	Lotus corniculatus	Lotus tenuifolius		
Scopoli	1772			lotus corniculatus		Lotus major	
Cavanilles	1793					Lotus pedunculatus	
Schkuhr	1796	Lotus rectus	Lotus hirsutus	Lotus arvensis			Lotus uliginosus

Table 1: Table of Equivalent Species

1824 and 1874 in which he classifies each previously described species as varieties of L. corniculatus.

He states:-

- "42. *L. CORNICULATUS* (Linn. spec. 1092)
caulibus prostratis, foliolis obovatis
vel linearibus glabris vel pilosis, stip-
ulis ovatis, bracteis lanceolatis linea-
ribusve, pedunculis longissimis, capitulis
depressis 8-10 floris, calycibus
campanulatis, laciutis aculis longitudine
tubi et corolla multo brevioribus,
leguminibus teretibus, seminibus renifor-
mibus viridi - atris. \mathcal{H} in pratis
Europae frequens. - Riv. t. 76. Fl. saepe
extus rubri exsiccatione virides. (v.s.)
- α *arvensis* (Ser. mss.) glabriusculus, caulibus
subprostratis, foliolis obovatis, floribus
luteis. - OEd. fl. dan. t. 991. *L. arvensis*
Schkuhr handb. 2. t. 211. (v.v.)
- β *major* (Ser. mss.) caulibus erectis plus
minusve pilosis majoribus fistalosis.
L. major Smith engl. bot. t. 2091. In
sepiibus humidis. *L. uliginosus* Schkuhr hand
2. t. 211. (v.v.)
- γ *villosus*, caulibus foliisque villosis
erectis, *L. villosus* Thuill. fl. par. ed.
2. p. 387. (v.v.)
- δ *crassifolius* (Pers. ench. 2. p. 354) pilosus,
foliolis ovatis carnulosis, caulibus
foliosis prostratis, radice crassa. - In
sterilibus maritimis. (v.v.)
- ϵ *Alpinus* (Schleich! cent. exs. n. 75)
caulibus foliisque minimis, floribus saepe
extus ruberrimis. In Alpiibus. (v.v.)
- ζ *tenuifolius* (Poll. fl. palat. 2. n. 711)
caulibus suberectis filiformibus, foliolis
stipulisque lineari-lanceolatis. - In
ruderatis. *L. tenuis* Kit! in Willd. enum.
p. 797. *L. depressus* et *humifusus* Willd.
enum. suppl. p. 52. ex Link enum. 2. p. 265.
(v.v.)
43. *L. PEDUNCULATUS* (Cav. ic. 2. p. 52. t. 164*)
glaberrimus, caule herbaceo, foliolis
lanceolatis acutis terminali petiolulato,
stipulis ovato-subcordatis, pedunculis
longissimis, floribus umbellato-capitatis,
bracteis lanceolatis acutis calyce subcampan-
ulato longioribus, laciniis calycinis subaeq-
ualibus acutis tubi longitudine et corolla
multo brevioribus, leguminibus.

*In Hispania. Flores flavi. An var.
L. corniculati?"*

"L. corniculatus (Linn.) prostrate stems, obovate leaflets, either glabrous or hairy, ovate stipules, lanceolate bracts, very long peduncles, flattened flowerheads, 8-10 flowers, bell-shaped calyx, tapering pods, kidney-shaped greenish seeds.

a. arvensis almost glabrous, almost prostrate stems, obovate leaflets, yellow flowers. L. arvensis Schkuhr.

b. major erect stems, more or less hairy, hollow stemmed. L. major Smith, in damp hedgerows, L. uliginosus Schkuhr.

c. villosus stems and leaves with erect hairs.

d. crassifolius distinctly hairy, fleshy/ovate leaflets, leafy prostrate stems, thick root. Found in infertile maritime regions.

e. alpinus very small stems and leaves, flowers very red on outside. In Alps.

f. tenuifolius stems thread-like and almost erect, leaflets and stipules linear-lanceolate. In rubbish dumps L. tenuis Kit. in Willdenow.

Lotus pedunculatus Cav. Very glabrous fleshy stem, lanceolate leaflets, the terminal leaflet being petiolated, stipules ovate with round basal lobes separated by a shallow notch, very long peduncles, umbellate flower heads, bracts sharply lanceolate, quite long with almost bell-shaped calyx. Calyx teeth pointed and of equal length, shorter than the corolla tube.... (as of Cavanilles).

Grows in Spain. Pale yellow flowers. Perhaps a variety of L. corniculatus?"

De Candolle proposes that L. arvensis and L. major, and possibly L. pedunculatus, should be regarded as varieties of L. corniculatus. He retains the distinction between the decumbent form named var. arvensis and the taller forms such as var. major. He fails to discriminate between L. major and L. uliginosus, making no reference to the spreading calyx teeth of L. uliginosus described by Schkuhr. He does however retain other previously recognised features of L. uliginosus such as the hollow stem and its

preference for damp habitats. In regarding L. uliginosus as synonymous with L. major de Candolle fails to contend with the inconsistency it creates with Scopoli's description of L. major as a plant of dry areas.

Introductions to the classification include var. crassifolius and var. alpinus. While both are smaller decumbent forms similar to L. arvensis, he distinguishes var. crassifolius on the basis of its fleshy leaflets, hairy appearance and maritime habitat. Var. alpinus is distinguished by its small leaflets and Alpine habitat.

The changes brought about by de Candolle are partly upheld by Gray (1821).

He states:

"Lotus major. Great birdsfoot-trefoil.
Heads depressed, 20-flowered; stem upright,
pipey, cylindrical; calyx-teeth bearded, bent
back; legumens cylindrical, spreading; claw of
the standard linear.

Lotus corniculatus major, *Raii Syn.* 334, 3.

Lotus uliginosus, *Hoffmann Germ.* 2, 100.

Lotus rectus, *De Candolle Fl. Gall.* 3939.

Lotus major, *Smith Engl. Bot.* 30, 2091.

Damp places and woods; perennial; June and July.

Stem 3 feet high; branches long, diffuse;
stipules nearly heartshape; flowers golden;
legumens tapering towards the end.

Lotus corniculatus. Horned birdsfoot-trefoil.
Head depressed, 8 to 10-flowered; stem decumbent,
solid; legumen spreading, stiff; claw of the
standard ovate.

Lotus corniculata glabra minor, *Raii Syn.* 334, 1.

Trifolium siliculosum minus, *Ger. em.* 1190, 5.

Lotus corniculatus, *Lin. S. P.* 1092.

Small coddled trefoil. Milk vetch.

Fields and pastures; also cultivated;
perennial; June to August.

Stem decumbent; opposite leaflets closed
together; flowers gold-colour; standard
fulvous; legumens larger towards the end. -
Herb, in moist meadows, makes excellent hay;

flowers turn green in drying, like those of indigo.

- β . tenuifolius. Stem long, slender, rather shrubby; leaves and stipules linear, lanceolate, bald; legumen slender.
Lotus pentaphyllus minor, angustioribus foliis, fruticosior, Raii Syn. 334, 2.
- γ . incanus. Leaves hoary, beneath.
Lotus corniculatus minor, foliis subtus incanis, Dill. in Raii Syn 334, 5.
- δ . glabra. Leaves bald; stipules semi-ovate; filaments clubshape.
Lotus corniculatus 6, Withering Bot. Arr. 808."

While retaining L. uliginosus as a synonym for L. major, he also includes L. rectus. The basis for this appears to have little historical justification. Gray combines descriptions suggestive of L. corniculatus i.e. heads depressed and legumes cylindrical and spreading, with others that suggest L. uliginosus i.e. calyx-teeth bent back and pipey stem.

L. rectus Linnaeus and L. rectus Schkuhr have rounded flower heads with upright pods, whereas L. major Scopoli has possibly pendulous pods.

By contrast, Gray's description of L. corniculatus remains the standard one for the decumbent form similar to L. arvensis DC or L. corniculatus L. He distinguishes three varieties on the basis of leaf shape and hairiness. He recognises var. tenuifolius as a slender-leaved variety as have other authors, and also a hairy form var. incanus and a glabrous form, var. glabra. Var. incanus may be equivalent to var. villosus DC, but not to L. hirsutus L. which was described as an upright plant.

The account by Smith (1825) in 'The British Flora' is particularly full and forms a reference point for later taxonomists.

He recognises three perennial species, L. corniculatus, L. major and L. decumbens.

He states:

"1. L. corniculatus. Common Bird's-foot-trefoil.

Heads depressed, of few flowers. Stems recumbent, pithy. Legumes spreading, nearly cylindrical. Claw of the standard obovate. Filaments all dilated.

In open grassy pastures, common.

Perennial. June-September.

Root branching, somewhat woody; the fibres beset with small granulations. Stems several, spreading on the ground in every direction, varying in length from 3 to 10 inches, simple or branched, solid, filled with pith, angular, leafy, sometimes quite smooth, but for the most part clothed, like the glaucous backs of the leaves, with close-pressed hairs. Leaflets obovate, acute, entire, on short partial stalks; the lateral ones oblique, or inequilateral. Common footstalk channelled, about the length of the leaflets, having at its base a pair of ovate stipulas, resembling them, but rather smaller. Flower-stalks axillary, solitary, erect or recumbent, angular, 5 times as long as the leaves, each bearing from 2 or 3 to 5 bright yellow flowers, dark green when dried, in a flat head or umbel, accompanied by a small ternate leaf. They change to orange in verging towards decay. The standard (not keel, as by a slip of the pen in Engl. Bot.) striped with red at the base in front; its claw much dilated and vaulted. Keel pale yellow. Filaments in their separate part all dilated under the anthers. Interstices of the calyx-teeth rounded. Legume smooth, of a shining purplish brown, a little depressed and channelled along the upper side.

L. corniculata glabra minor. Raii Syn. 334. Bauh. Hist. v. 2. 354. f. 355.

L. sativa. Dalech. Hist. 507.

Trifolium siliquosum minus. Ger. Em. 1190 f.

T. corniculatum primum. Dod. Pempt. 573. f.

Melilotus germanica. Fuchs. Hist. 527. f.

M. nobilis. Trag. Hist. 594. f.

Meliloti tertium genus. Fuchs. Ic. 299. f.

β. Lotus corniculata minor, foliis subtus incanis.
Dill. in Raii Syn. 334.

L. corniculatus ε. Fl. Br. 794. "

It can be seen that this description covers the range of previously described decumbent forms including L. arvensis, L. crassifolius and possibly var. incanus.

Smith again raises the question of the attitude of the pods. Initially he describes them as 'spreading', and later enlarges on this when he states that they are 'a little depressed'. This may have seemed to Smith to be a satisfactory compromise after considering the previous difficulties other authors had had with this character.

Smith's description of Lotus major is:

"2. L. major. Greater Bird's-foot-trefoil.

Heads depressed, many-flowered. Stems erect, tubular. Legumes drooping, cylindrical. Claw of the standard linear. Shorter filaments not dilated.

L. major. Scop. Carn. v. 2. 86. Comp. ed.

4. 124. Engl. Bot. v. 30. t. 2091. Pursh. v.

1. 342. Forst. Tonbr. 86. Grev. Edin. 163.

L. corniculatus δ . Fl. Br. 794.

L. corniculatus β . Hook. Scot. 220.

L. n. 385 α . Hall. Hist. v. 1. 167.

Loti corniculatae major species. Rati Syn. 334.

Bauh. Hist. v. 2. 355. f. 356.

Lotus. Riv. Tetrap. Irr. t. 76. f. 1.

β . L. pentaphyllos medius pilosus. Dill. in

Rati Syn. 334.

L. corniculatus δ . Fl. Br. 794."

Smith's view is an interesting combination of ideas. In all respects it represents the views held by de Candolle and Gray, with the one exception of the attitude of the pods. He states that L. major has drooping pods, his description reverting back to the original observation by von Haller and used by Scopoli. This is in direct contrast with Gray's opinion that L. major is synonymous with L. uliginosus and L. rectus and therefore by inference has

straight or upright pods.

Smith quite clearly does not regard L. major as a form of upright corniculatus, as might have been the case, having given it equivalence in some respects with L. major Scopoli. Whereas Scopoli thought of L. major as a plant of dry areas, to Smith it is quite different and L. uliginosus-like in its choice of habitat. Smith states, contrasting it with L. corniculatus, that:

"It is a plant of wet bushy places, and hedges. Very different from the foregoing species (L. corniculatus) in general habit, and now technically distinguished by several clear and sufficient characters, for most of which I am indebted to the worthy Dean of Bristol. Every botanist had been struck with the aspect of the plant, and Scopoli long ago proposed it as a species, but without a sufficient specific definition, except that of the shorter separate filaments not being, like the longer ones, dilated under their anthers. The stems are from 1 to 2 or 3 feet high, upright, clothed, more or less, with long loosely-spreading hairs, rarely quite smooth; internally hollow, or tubular, with little or no pith in any part, which I take to be an important character. Leaves fringed or clothed with similar hairs. Fl. from 6 to 12 in each head, of a duller orange than the former. Calyx-teeth stellated in an early state; their interstices, when fully expanded, acutangular, not rounded. Claw of the standard almost linear, though vaulted. Legumes not horizontal, but drooping, slender and exactly cylindrical.

Whether there may be any difference in the agricultural qualities of these plants, and whether the present might be capable of cultivation in very wet meadows, nobody has hitherto inquired."

These views are supported by Lindley (1829) and Withering (1830), both of whom agree on the moist habitat of L. major. The third

species, L. decumbens, described by Smith makes an interesting, if diverting, contribution to classification of the group.

He states:

"L. decumbens. Spreading Bird's-foot-trefoil

Heads of few flowers. Stems recumbent, nearly solid. Legumes somewhat spreading, cylindrical, two-edged. Calyx hairy; its teeth shorter than the tube.

L. decumbens. Forst. Tonbr. 86. Stems widely spreading, partly quite prostrate, a foot or more in length, branched, filled with light pith, angular, leafy, smooth, somewhat glaucous. Leaves glaucous, smooth above; occasionally clothed beneath with short, close, bristly hairs. Leaflets and stipulas similar, lanceolate, pointed, oblique, except the terminal one, which is obovate-lanceolate. Common footstalk but half the length of the leaflets, channelled, slightly bordered. Flower-stalks axillary 4 or 5 times the length of the leaves, smooth, stout and firm, obscurely angular, each bearing an umbel of from 3 to 6 bright yellow flowers, accompanied by a ternate leaf without stipulas. In starved plants the flowers are solitary. Partial stalks and calyx all over silky, with more or less abundant, short, close hairs; the calyx-teeth lanceolate, tapering, spreading, shorter than the tube, somewhat hairy, with wide rounded interstices. Separate portion of each filament of considerable length, the longest dilated upwards. Legumes nearly erect, or but slightly spreading, smooth, dotted, cylindrical, without any depression or channel, both sutures rather prominent, forming a ridge along each margin.

I can find no account of any thing approaching this species except L. pedunculatus, Cavan. Ic. t. 164, the plate and description of which are not very discriminative, but its stem is said to be erect, 3 feet high, and every part of the plant is perfectly smooth. L. decumbens grows in Switzerland and the Levant, as well as on the sandy shores of Sicily. Most botanists have supposed it a variety of the corniculatus."

That most botanists had supposed it a variety of L. corniculatus could not have surprised Smith for it is very similar to his own

description of L. corniculatus. Apart from having lanceolate and not obovate leaflets, in many ways L. decumbens is reminiscent of L. crassifolius as described by de Candolle, particularly as both L. crassifolius and L. decumbens had been observed in maritime habitats.

Why Smith should associate L. decumbens with L. pedunculatus Cavanilles is not clear. Except for having lanceolate leaflets it appears as quite different. L. decumbens is a prostrate, partly hairy plant with stems around 1 foot. L. pedunculatus is erect, glabrous, with stems 3 feet tall. Smith himself makes this comparison.

By 1830, Hooker in 'British Flora' had questioned Smith's classification and incorporated L. decumbens with L. tenuis.

"2. L. tenuis, Waldst. et Kit. (Slender Bird's-foot trefoil); heads depressed umbellate 6-10-flowered, stems prostrate slender, leaflets lanceolate, peduncles very long, claw of the standard inflated above. Borr. et Hook. in Engl. Bot. t. 2615. - L. corniculatus, var. tenuifolius, Poll. - De Cand. - L. decumbens, Forst. Tonb. 86."

He remains uncertain however of the distinction of L. tenuis and L. corniculatus, possibly because of his inclusion of L. decumbens and further states of L. tenuis:

"I am really unable to point out any marks by which this may be known from the preceding (L. corniculatus) except its more slender and straggling habit, and narrower foliage. It is certainly by no means an uncommon plant."

With similar doubts in mind Hooker writes of L. major:

"Sides of ditches and moist bushy places, by no means unfrequent. Fl. July, Aug. . . The place of growth of this plant, in moister situations than *L. corniculatus*, consequently inducing a greater development of every part, is I think, in itself, almost sufficient to account for those trifling differences which are said to distinguish it from that well-known species. The difference of breadth of the filaments in the two, mentioned by Smith, Mr. Wilson finds not to be constant. *L. corniculatus*, he adds "seems to differ chiefly in the vaulted or gibbous appearance of the upper part of the claw of the standard, which raises up the two teeth of the calyx above." But is this mark constant? Smith says the claw of the standard of our present plant, "though linear, is vaulted."

This concern over the constancy of characters does not escape the notice of Withering (1830). In his publication 'British Plants' he makes the following observation on the genus:

"It is, perhaps, more difficult to give a true and Essential Character to this genus, than to any other, notwithstanding the general habit, which is at once perceptible, and the properties of the plants which compose it show that it is a natural one; and those who have attempted to divide it, have not been able to fix any certain limits to their subdivisions."

Despite these reservations he later makes a positive contribution to the discussion by including the results of a colleague working with both *L. corniculatus* and *L. major*:

"Mr. Sinclair states that he has raised this plant from seed on two different soils, the above characters remaining permanent (i.e. those described by Hooker) and expresses his surprise that two plants so distinct in habits should have so long been considered varieties only. "What renders a specific distinction of most importance to the farmer, is the difference which exists between them

in an agricultural point of view. The weight of green food, or hay, produced by *L. major* is triple that of *L. corniculatus*, and its nutritive powers are little inferior, but it is extremely bitter. It does not appear to be eaten by any cattle when in a green state; but when made into hay with common grasses, sheep, oxen, and deer eat it without reluctance. In moist clayey soils it would doubtless be a most profitable substitute for red clover, but the excess of bitter extractive and saline matters it contains seems to forbid its adoption without a considerable admixture of other plants." Hort. Gram. E.)."

The German botanist Koch (1843) showed that the current European opinion concurred with that of most British authors:

"L. CORNICULATUS (L. sp. 1092) procumbens glaber vel hirsutus, pilis patentibus, pedunculis folio quadruplo quintuplo longioribus, capitulis subquinquefloris, dentibus calycis e basi triangulari subulatis subaequalibus ante anthesin conniventibus, alis lato-obovatis, carina subrhombea rectangule adscendente, leguminibus linearibus teretibus rectis. 4. In pascuis, pratis, ad sylvarum oras. Mai.-in autumn. L. arvensis Schk. t. 211. Flores lutei, extus saepe sanguinei, raro toti sanguinei. Foliola et stipulae obovata. Variat:

- α. vulgaris, glaber vel sparse pilosus.*
- β. ciliatus, foliolis calycibusque pilis longis ciliatis.*
- γ. hirsutus, totus hirsutus. L. villosus Thuill. par. ed. 2. p. 387.*

L. TENUIFOLIUS (Rohb. fl. exc. p. 506) procumbens glaber vel subhirsutus, pilis patentibus, pedunculis folio quadruplo quintuplo longioribus, capitulis subquinquefloris, dentibus calycis e basi triangulari subulatis subaequalibus ante anthesin conniventibus, alis oblongo-obovatis, carina subrhombea rectangule adscendente, leguminibus linearibus teretibus rectis. 4. In pratis, praecipue locis salsis, (zerstreut dch. d. g. Gebiet). Mai in autumn. L. corniculatus γ. tenuifolius L. sp. 1092., (sec. herbar. C. Bauhini, conf. Hagenb. fl.

basil. 2. 244). *L. corniculatus* γ.
tenuifolius Pollich. pal. 2. p. 349.,
 var. δ. Koch. syn. ed. 1. p. 179.
L. tenuis Kit. in Wild. en. h. berol. 2.
 797. *L. decumbens* Forster. in Smith.
 engl. fl. 3. 314. Engl. bot. t. 2615.,
caulis anguste fistulosus, foliola et
stipulae linearia vel lineari-obovata.
Alae evidenter angustiores, quam in
L. corniculato, "atque hac sola nota
L. tenuifolius statim a praecedente dig-
noscitur." Petermann., fl. lips. p. 540.,
quod in speciminibus siccis ipse observo.

L. ULIGINOSUS (Schkuhr. t. 211) *erecti-*
usculus, glaber vel subpilosus, pilis
patentibus, capitulis sub 12 floris longe
pedunculatis, dentibus calycis e basi
triangulari subulatis subaequalibus
corollam dimidiam aequantibus ante
anthesin reflexis, carina e basi ovata
sensim in rostrum attenuata, leguminibus
linearibus teretibus rectis. ♀. In fossis
et pratis paludosis. Jul. Aug.
L. major Smith. engl. fl. 3. 313. Koch syn.
 ed. 1. 178. D. fl. 5. 306. *L. vindicatus*
 Böningh. cat. sem. hort. monast. 1829. (*L.*
major Scop. carn. 2. p. 86., sec. descrip-
 tionem ad aliam plantam pertinere videtur.)
 Differt a *L. corniculato*: caule altiore,
 evidenter fistuloso, capitulis magis multi-
 floris, directione dentium calycis ante
 anthesin, vexillo ovato, non subrotundo,
 alis carinam angustiore, haud subito in
 rostrum angustatam, in planta viva penitus
 tegentibus, (carina deorsum intra alas
 eminet in *L. corniculato*), legumine duplo
 fere angustiore et seminibus copiosioribus
 dimidio minoribus. Filamenta longiore non
 differunt et in hac et in antecedentibus
 apice valde dilatata sunt."

"*L. corniculatus*. Decumbent, glabrous or hairy, with spreading
 hairs, peduncles longer with a 4 or 5 fold leaf, heads upto 5
 flowered, with sharply pointed calyx teeth, almost even in length
 arising from a triangular base, closed together before flowering,
 wings laterally obovate, keel almost rhomboid with a rectangular
 standard, legumes linear, tapering, straight. In pastures,
 meadows, edges of woods, May-autumn. *L. arvensis* Schk. Flowers
 yellow, outside often red, rarely completely red. Leaves and
 stipules obovate. Varieties

α *vulgaris*; glabrous or sparsely hairy.

β *ciliatus*; hairy or very hairy.

γ *hirsutus*; completely hairy *L. villosus* Thuill.

L. tenuifolius. Decumbent glabrous or partly hairy, with spreading hairs, peduncles longer with a 4 or 5 fold leaf, heads upto 5 flowered, with sharply pointed calyx teeth, almost uniform in length, arising from a triangular base, closed together before flowering, wings laterally obovate, keel almost rhomboid with a rectangular standard, legumes linear, tapering, straight. In meadows chiefly in salty areas. Narrow, hollow stem with linear or linear-obovate leaflets and stipules. The wings evidently narrower than in L. corniculatus, and by this single characteristic L. tenuifolius is immediately distinguishable from the preceding plant.

L. uliginosus Schk. Somewhat erect, glabrous or slightly hairy, hairs spreading, about 12 flowers per head, very long peduncles, calyx teeth arising from a triangular base, almost even in length, equal to half the length of the corolla tube, bent back before flowering, the keel ovate at base gradually narrowing towards tip, linear, straight, tapering legumes. In ditches and marshy meadows.

It differs from L. corniculatus by: taller stems, obviously narrow, many more flowers on umbels, the direction of the calyx teeth before flowering, ovate standard, not rounded, with wings covering a narrower keel which is not abruptly tapering but is completely enclosed in the living plant (the keel is visible below the wings in L. corniculatus), by pods almost twice as narrow and seeds many but half the size. Filaments are not different in length, and in this and the previously mentioned species the tips are greatly dilated."

Koch's description of L. uliginosus clearly follows that published by Schkuhr, and like Smith, Gray and De Candolle, he associates it with L. major Scop.

As L. corniculatus is taken to be a smaller, decumbent plant, in the absence of any description of an upright L. corniculatus it is almost inevitable that such taller forms could be mis-identified as L. uliginosus.

The failure to discriminate between these two forms suggests the difficulty involved in being able to do so. However, it is possible to extract from previous descriptions some characters that are more helpful than others.

Those, the more commonly described characters retained over the years, would appear to have the most useful diagnostic

value. The ones which appear most frequently for distinguishing between plants at a specific level are: growth habit, appearance of calyx teeth and number of flowers per inflorescence. Other characters, particularly degree of hairiness and leaflet shape are more favoured for their intra-specific value. By 1850 characters such as length, shape and attitude of the filaments, petals and legumes appear to have been dismissed as unreliable.

This re-evaluation of the taxonomic characters is reflected in the descriptions published by Hooker & Arnott (1850) in 'The British Flora' and by Babington (1843 and 1851) in 'Manual of British Botany'. Babington's description is as follows:

- "1. L. corniculatus (L.); claw of the standard obovate transversely vaulted, calyx-teeth straight in the bud subulate from a triangular base, points of the 2 upper ones converging, heads 5-10-flowered. - Glabrous or slightly hairy. Stem ascending. Leaflets obovate. Stipules ovate. Angle between the 2 upper calyx-teeth rounded. - β. villosus (Ser.); upper part of stem., leaves., and calyx hairy with long spreading hairs. - γ. crassifolius (Pers.); pilose, stem caespitose, leaflets obovate fleshy, stipules ovate. - δ. L. tenuis (Sm.); glabrous or slightly hairy, stem filiform elongated procumbent or ascending, leaflets linear or linear-obovate, stipules 1/2-ovate. - Pastures, dry banks.
2. L. major (Scop.); claw of the standard linear, calyx-teeth spreading like a star in the bud subulate from a triangular base, two upper ones diverging, heads 8-12-flowered, leaflets obovate, stipules roundish-ovate.
L. uliginosus Schkuhr. - Hairy. Stem usually erect, 1-3 feet high. Angle between the 2 upper calyx-teeth acute. - β. glabriusculus (Bab.); glabrous, the margins and nerves of the leaves stipules bracts and sepals ciliated, stem erect or procumbent. - In damp places.
β. on drier spots."

Babington's classification is interesting for two main reasons.

Firstly, he introduces a new feature contrasting the difference between the calyx teeth of L. corniculatus and those of L. major. He mentions the angle set by the upper two calyx teeth; a diagnostic character in modern use. Secondly, Babington recognises a more glabrous form of uliginosus, erect or procumbent, a plant of drier areas. Possibly var. glabriusculus could go part way to providing the missing description for an upright L. corniculatus.

Such distinctions did not find universal agreement, for Bentham (1858) in his 'Handbook of the British Flora', names only one species, L. corniculatus L., and writes:

"It is a very variable species, accommodating itself to very different stations and climates; and some of the races appear so permanent in certain localities as to have been generally admitted as species, but in others they run so much into one another as to be absolutely undistinguishable."

Bentham's opinion is acknowledged by Hooker and Arnott (1860) in a later edition of their work. Hooker in fact restates his reservations, held since 1830 concerning L. major.

"The place of growth of this plant, in moister situations than L. corniculatus, consequently inducing a greater development of every part, is, in itself, almost sufficient to account for the trifling variations which distinguish it from that well-known species, to which it has been united by Mr. Bentham. It is sometimes nearly glabrous, but usually hairy; and a very hairy state has been gathered in Ireland."

From this time on, the specific epithet 'major' is gradually superseded by its acknowledged synonym, 'uliginosus'.

In Europe, Wagner (1871) in 'Deutsche Flora' and Bouvier

(1878) in 'Flore de Alpes' had both retained L. major Scop. But by 1889 Gremlé in 'The Flora of Switzerland' and later Willkomm (1893) in 'Prodromi Florae Hispanicae, Supplementum', had both preferred the use of L. uliginosus Schk.

Of importance is the observation made by Willkomm after his description of L. uliginosus.

"3720^{bis} (lapsu 3719). *Lotus uliginosus* Schk. Adde:
β. brachycarpa Wk. in litt., leguminibus
brevibus (12-15 mm l.). Prope Ronda ad ripas
fluv. Rio del Tajo (REVERCH. 1889) et in
humidis pr. Grazalema (REVERCH. 1890, forma
latifolia, caulibus hirsutis).
Observ. Ad hanc speciem certe referendus est
L. pedunculatus Cav. qui nil est nisi forma
glabra foliolo medio plus minus longe
pedicellato."

"Lotus uliginosus Schk.

β. brachycarpa Wk. in litt. with short legumes (12-15mm).
Beside Ronda near the river banks of the Rio de Tajo (Reverch. 1889) and in wet meadows of Grazalema (Reverch. 1890, a broad-leaved form with hairy stems).

Observation. This species is certainly called to mind by L. pedunculatus Cav. which is none other than a glabrous form with medium-sized leaves and more or less long pedicels."

The revival of L. pedunculatus and its linking with L. uliginosus added a further dimension to the classification of the group which was later to be the subject of some controversy.

Although in Britain the matter of L. pedunculatus had yet to be considered, clearly Bentham also took a broad view of the group. In a revised edition (1900) of 'The Handbook of British Flora', he remains firmly of the opinion that L. corniculatus is an aggregate species with a number of forms.

He writes:

"a. L. uliginosus, Schk. Tall, ascending or

nearly erect, glabrous or slightly hairy, and luxuriant in all its parts, with 6 to 8 flowers in the umbel. Calyx-teeth usually, but not always, finer and more spreading than in the smaller forms. In moist meadows, along ditches, under hedges, and in rich, bushy places. L. major, Sm.; L. pilosus, Becke.

b. L. crassifolius, Pers. Low and spreading often tufted at the base, glabrous or nearly so, usually with 5 or 6 rather large flowers to the umbel. Leaflets broad, and often glaucous, especially near the sea, where they become much thicker. In open pastures and on dry, sunny banks.

c. L. villosus, Coss. and Germ. Like the common variety, but covered with long spreading hairs. In dry, sunny situations, common in southern Europe, but in Britain found only in Kent and Devon.

d. L. tenuis, Waldst and Kit. Slender and more branched than the common form, with very narrow leaflets. In poor pastures and grassy places, chiefly in south-eastern Europe. Rare in Britain, and always running much into the common form. L. decumbens, Forst."

It is apparent from Bentham's description of L. uliginosus, the only upright form, that he does not regard the spreading calyx teeth as an altogether consistent character. On this description, taller, ascending forms with straight calyx teeth, perhaps better described as an upright L. corniculatus, could be included.

It cannot be assumed that such upright forms, while existing in continental Europe, did not also exist in Britain. Herbarium material of exactly this type, collected in Bullington, Oxfordshire, in 1893, and identified as L. uliginosus var. glaber, exists at the Royal Botanic Garden, Edinburgh.

This problem of distinguishing between these two forms, L. uliginosus and upright L. corniculatus was addressed by Hegi (1907) in 'Illustrierte Flora von Mittel-Europa'. Hegi gives an

extensive and detailed account of the group. Although he only distinguishes two species, L. corniculatus and L. uliginosus, he splits L. corniculatus into a number of sub-species, varieties and forms. Among these is the sub-species major

"3. subsp. major (Scop.) (= L. major Scop., = L. vindicatus Boenigh., = L. angustifolius Guldenst., = L. intermedius Deslong, = L. tenuifolius var. odoratus Boiss.). Stengel 2 bis 3 dm hoch, aufsteigend oder aufrecht, weitrohrig, meist ziemlich lang behaart, astig, bis oben beblättert. Blättchen meist lanzettlich, die unteren länglich-lanzettlich. Blütenstände kurz gestielt, meist 2- bis 4- (bis 6-) blütig. Blüten ziemlich klein. Kelchähne schmal, + so lang wie die Kelchröhre. Südosteuropa (Polauer Berge in Mähren, Krain, Istrien, Balkanländer), Asien, Nordafrika (bis Aegypten und Abessinien)."

"L. corniculatus subsp. major Scop = L. major Scopoli

Stem 2 to 3 dm high, upright to erect hollow stem with quite long hairs, leafy to the top of stem. The small leaves are mostly lanceolate with the lower ones linear-lanceolate. Peduncles are short-stemmed, mostly with 2 to 4 but upto 6 flowers. Flowers are quite small. Calyx teeth narrow, more or less as long as the calyx tube."

Hegi contrasts this with L. uliginosus.

"1877. Lotus uliginosus) Schkuhr (= L. major Sm. non Scop., = L. corniculatus L. var. major Ser. und subsp. uliginosus Pers., = L. odoratus Holl in Hook., = L. pisifolius Lowe, = L. nummularius Rehb.). Sumpf-Hornklee, Hoher Schotenklee, Gehornter Sumpfklee.

Engl.: Greater bird's-foot trefoil. Fig. 1432 f bis 1 und 1433 a, b.

Ausdauernd, mit kurzlebiger Pfahlwurzel und langen, mit Niederblättern besetzten, wurzelnden Bodenausläufern (Fig. 1433a und b); aus diesen die Laubsprosse entspringend. Stengel aufsteigend oder aufrecht, 3 bis 9 dm hoch, oft ziemlich stark verzweigt, schwach (daher sich oft an hohen Gräsern und Stauden stützend),

meist weitröhrig, schwach gerillt, kahl oder + behaart. Laubblätter dicklich, oberseits lebhaft, unterseits bläulichgrün, ähnlich denen der vorigen Art, doch die Blättchen etwas grösser, mit deutlichen Seitennerven, die oberen oft mehr elliptisch, die unteren nebenblattförmigen breit schief-herzförmig, alle am Rand oft gewimpert. Blütenstandsstiele kräftig, 3 bis 4 mal so lang als das tragende Laubblatt. Blütendolden meist 8- bis 12- (4- bis 15-) blutig, am Grund mit 1- bis 3-zähligen Hochblatt. Blüten meist radial ausgebreitet, + 13 mm lang, deutlich gestielt. Kelch 5- oder 10-nervig; die Zähne so lang oder etwas kürzer als die Röhre, lineal, weniger spitz als bei *L. corniculatus*, oft bewimpert, vor dem Aufblühen bogenförmig abstehend bis fast sternförmig ausgebreitet."

"*L. uliginosus* Schkuhr = *L. major* Smith non Scopoli

Stem upright, 3 to 9 dm high, often quite well branched, weak and often found among tall grasses, mostly hollow, slightly grooved, glabrous or more or less hairy. Foliage leaves thickish, upperside bright green, bluish-green on undersurface, leaves similar to sub sp. major but bigger with clearly marked veins. The upper leaves are often more elliptical, the lower leaves, as are the stipules, almost heart-shaped, the terminal leaflets often ciliate. Peduncle erect, 3 to 4 times as long as the leaves. Flower heads mostly 8 to 12 (14-15) flowered, subtended by a leaf divided 1 to 3 times. Flowers mostly radially arranged, about 13mm long, clearly stemmed. Calyx 5 or 10 nerved, the teeth are as long as or slightly shorter than the tube, not as pointed as *L. corniculatus*, before the flower opens the teeth are bent backwards as of a star."

It is Hegi's opinion that there is a difference between *L. major* Smith and *L. major* Scopoli. Whereas he finds *L. major* Smith to be synonymous with *L. uliginosus* Schkuhr, as do previous authors, Hegi prefers *L. major* Scopoli to be used to describe an upright *L. corniculatus*. This would appear to fit with Scopoli's view who refers to Bauhin's naming of the plant as *Lotus corniculatus* major species (Page 12).

It was Smith himself who felt that *L. major* Smith and *L. major* Scopoli were the same (Page 27) although Babington also

appears to have had doubts. He lists L. major (Scop?) separately from L. uliginosus Schkuhr (Page 35).

This point is discussed by the American author, MacDonald (1946) in his book 'Bird's-foot Trefoil: its Characteristics and Potentialities as a Forage Legume',

"Considerable difficulty and confusion has existed concerning the nomenclature of L. uliginosus. Continental European writers have followed the example of Brand (1898) describing the plant as greater or marsh bird's-foot trefoil under the name L. uliginosus Schkuhr, while British authors generally have given it the name Lotus major Smith. American writers have for the most part, followed the former nomenclature."

MacDonald goes on to say,

"Brand contends that L. major Scopoli is not L. major Smith = L. uliginosus Schkuhr. He feels that the descriptions given in each instance did not apply to the same species. He did not, however, compare herbarium specimens."

Prior to MacDonald, Robinson (1934) in "Birdsfoot Trefoil: A Monograph", had also discussed the matter and argued the reverse.

"If we examine Bauhin's work we find the plants now known as L. corniculatus and L. major both described and also illustrated. There can be no doubt that the illustration accompanying "Loti corniculi major species" refers to L. major Sm. = L. uliginosus Schk. It differs from L. corniculatus in having more numerous and smaller flowers (despite the text which speaks of "flores...in orbe congesti, majiores") and the drawing shows in one case 8 fruits per head, and in another case 7 fruits per head, numbers which are unusual in L. corniculatus but common in L. major."

Robinson concludes that

"it is permissible to adopt Smith's version, despite the authority of Brand, and call the Greater Birdsfoot Trefoil, Lotus major Scop. sec. Smith = L. uliginosus Schkuhr, in view of the fact that the latter name is of more recent origin.

Brand says that European botanists have little difficulty in distinguishing between the two species, but when considering extra-European forms it is not possible to draw a sharp distinction between them. He lays great stress on the lateral veins of the leaflet, which in L. major are distinct while the reverse is the case in L. corniculatus."

Hegi (1907), also points out that the leaf veins of L. uliginosus = L. major Smith are clearly visible and finds it a useful character for distinguishing between L. uliginosus and L. corniculatus ssp. major = L. major Scopoli.

While in Continental Europe these distinctions were being discussed, contemporary workers in North America were still content to provide broad descriptions of L. corniculatus. Britton & Brown (1897) in 'An Illustrated Flora of the Northern U.S. and Canada', provided the following description:

"Lotus corniculatus L. Bird's-foot Trefoil.
Ground Honeysuckle. Bloom-fell.
Lotus corniculatus L. Sp. Pl. 775. 1753.
Perennial from a long root, appressed-pubescent or glabrate. Stems slender, decumbent, or ascending, 3'-2⁰' long; leaves 3-foliate, short-petioled; leaflets obovate, oblanceolate or oblong, 3"-8" long, obtuse or acute; stipules similar to the leaflets, and often as large; peduncles elongated, sometimes 4'-6' long, umbellately 3-12-flowered; calyx-lobes acute, as long as the tube or shorter; corolla bright yellow, 6"-9" long, or the standard reddish; pods linear, about 1' long, spreading, several-seeded.

In waste places and on ballast, New Brunswick, and about the seaports of the Eastern and Middle States. Adventive from Europe. Native also of Asia, and widely distributed as a weed. Crowtoes (Milton), Cat's-clover, Sheepfoot. June-Sept."

While making a reference to Linnaeus's description of the decumbent form of L. corniculatus, they also include ascending forms with upto 12 flowers. Such large numbers of flowers are more commonly found in L. uliginosus, which is not described separately.

Not all Europeans followed the example set by Hegi either, for Coste (1937), although recognising L. uliginosus Schk. as synonymous with L. major Sm., also provides an all-embracing description of L. corniculatus.

"L. CORNICULATUS L. - Plante vivace de 10-40 cm., glabre ou velue à tous les degrés, à souche dure; tiges pleines ou à peine creuses, couchées ou ascendantes; folioles obovales ou oblongues; stipules ovales; fleurs jaunes, verdissant par la dessiccation, 3-6 sur des pedoncules bien plus longs que la feuille; calice en cloche, à dents égales, triangulaires en alène, dressées-conniventes même dans le bouton, égalant le tube; ailes obovales, à bord inférieur fortement courbé: carène courbée presque à angle droit; gousse de 20-35 mm., linéaire, un peu épaisse, droite. Plante polymorphe.

Prés, bois, champs, coteaux, dans toute la France et en Corse. - Europe; Asie; Afrique septentrionale. = Mai-septembre."

"L. corniculatus L. - Perennial plant - 10-40cm, glabrous or somewhat hairy, with a woody root stock, stems solid or slightly hollow, decumbent or ascending. Leaflets obovate or oblong, stipules oval, flowers yellow, becoming green when they dry out, 3-6 on peduncles much longer than the leaf.

Calyx bell-shaped, teeth of equal length, triangular tapering to a point, erect, gradually converging, even in the bud, the same length as the tube; obovate wings, with the lower edge sharply curved, keel is curved to the extent of being almost a right angle: pods of 20-35 mm, linear, somewhat thickened, straight. Polymorphous plant.

Meadows, wood, fields, slopes, throughout France and Corsica, Europe, Asia, North Africa, (Flowers) May-Sept."

Coste, although recognising the type of plant described by Hegi as L. corniculatus ssp. major, does not distinguish it from decumbent forms. Instead he prefers to point out that the plant is polymorphous.

In 1941 Binz and Thommen published their description in 'Flore de la Suisse'.

"*L. corniculatus* L. - 10-30 cm. Pl. glabre ou pubescente. Tige ascendante, anguleuse. Fol. obovales à oblongues ou (ssp. *tenuifolius* [L.] Hartman) linéaires-oblongues. Ombelles à 3-8 fl. Cal. à dents conniventes avant la floraison. Cor. jaune, souvt lavée de rouge. - 5-7. - Prés, chemins; très fréq.
L. uliginosus Schkuhr - 30-50 cm. Pl. glabre ou parsemée de poils épars. Tige dressée ou ascendante, cylindrique, fistuleuse. Ombelles à 8-15 fl. Cal. à dents réfléchies avant la floraison. Cor. jaune. - 6-7. - Lieux marécageux, bois humides; rép."

"*L. corniculatus* L. 10-30cm. Glabrous or pubescent plant. Stem ascending, angular, leaflets obovate to oblong or (ssp. *tenuifolius* [L.] Hartman) linear oblong. Flower heads with 3-8 flowers. Calyx with teeth converging before flowering. Yellow corolla, often tinged with red. (Flowers) 5-7. Meadows, lanes; very frequent.

L. uliginosus Schkuhr - 30-50cm. Plant glabrous or with a scattering of thin hairs. Stem upright or ascending, cylindrical, fistular. Flower heads with 8-15 flowers. Calyx teeth curved back before flowering. Yellow corolla - 6-7. Marshy sites, damp woods; widespread."

Rather surprisingly Binz and Thommen fail to recognise any decumbent form of L. corniculatus such as L. crassifolius or

L. alpinus, particularly as such a plant had previously been described in Switzerland by Thompson in 1912. In his 'Sub-Alpine Plants of the Swiss Woods and Meadows', he stated:

"Lotus corniculatus L. Bird's-foot Trefoil.

A small glabrous plant, 3-8 inches high, tufted, but very variable in habit.

Leaves very shortly petioled. Flowers very shortly pedicelled, bright yellow, often streaked with crimson and turning green when dry, 5-10 flowers in a decumbent umbel or head about an inch across, on long peduncles; 2 upper calyx teeth triangular. Pods about an inch long.

Pastures from the plains to 9000 feet (var. alpinus Schl.) in the Alps. May to July.

Distribution. - Europe, to the Arctic regions, N. Africa, N. and W. Asia, India."

The existence of L. alpinus Schleicher had previously been discussed by Hegi (1907). By 1950 Hegi's views still influenced the classification of the group and were re-stated by the Czech botanist Dostál (1950). Although mentioning the absence of L. uliginosus in Slovakia he draws useful and clear distinctions between L. corniculatus and L. uliginosus.

"Lodyhy plně n. úzce duté, lístky bez postranních žilek, dol. šikmo vejčité; kvetenství 2-5 květé, K. cípy dovnitř skloněné, člunek dl. zobánkatý:
L. corniculatus.

Lodyhy zřetelně duté, lístky se zřetelnými postranními žilkami, dol. okrouhle srdčité, kvetenství nejméně 10 květé, K cípy rozestálé až nazpět ohnuté, člunek znenáhla zašpičatělý:
L. uliginosus."

"L. corniculatus

Stems solid or narrowly hollow with pith; lateral veins of leaflets not obvious; stipules obovate, set at slight angle; 2-5 flowers in inflorescence; calyx teeth turned inwards; keel long and tapering to a point.

L. uliginosus

Stems distinctly hollow; leaflets with obvious lateral veins; stipules ovate; 10 flowers in inflorescence; calyx teeth turned outwards; keel comes abruptly to a point."

Dostál also describes 3 sub-species of L. corniculatus: ssp. tenuifolius; ssp. euorniculatus, a solid-stemmed decumbent form; and ssp. major, a slightly hollow-stemmed upright form of dry sunny positions. This later description is the same as that proposed by Hegi (1907) for ssp. major Scopoli non Smith.

In Britain at this time, few if any authors had distinguished between the decumbent and ascending or upright forms of L. corniculatus. However all recognised L. uliginosus and L. tenuis as being distinct forms, if not separate species, with general agreement about the characters involved.

Hutchinson (1955) and Melderis & Bangerter (1955) refer to L. corniculatus as a plant with decumbent or ascending stems upto 1 foot. However McClintock & Fitter (1956) state that it is usually prostrate whereas Butcher (1961) refers to ascending stems of 3 to 6 inches. Clapham, Tutin & Warburg (1962) were of the opinion that British L. corniculatus was of a decumbent form. The classification also reveals Tutin's decision to change the nomenclature of L. uliginosus used in the first edition (1952) to L. pedunculatus Cavanilles.

His descriptions are as follows:

"L. corniculatus L. Birdsfoot-trefoil, Bacon and Eggs. A decumbent almost glabrous or rarely hairy perennial 10-40 cm. Rootstock stout, scarcely stoloniferous,

stem solid or nearly so. Lflets 3-10mm., obovate, obtuse or apiculate, lower pair broadly ovate or lanceolate; petioles short. Heads (1-)2-6(-8)-fld; peduncles up to c. 8cm., stout. Fls c. 15mm., yellow, often streaked or tipped with red, shortly pedicelled. Calyx-teeth triangular, erect in bud, two upper with an obtuse sinus. Petals 2-3 times as long as calyx. Pod up to 3cm. Fl. 6-9. $2n = 24^*$. Hp. Variable.

Native. In pastures and grassy places. 112, H40, S. Generally distributed throughout the British Is. Europe to about 71° N.; Asia; N. and E. Africa; in the tropics only on mountains.

L. pedunculatus Cav. 'Large Birdsfoot-trefoil.'

L. uliginosus Schkuhr; L. major auct.

An erect or ascending glabrous or pubescent perennial 15-60(-100)cm. Rootstock slender, producing numerous stolons. Stem hollow. Lflets usually 15-20mm., obovate, often obliquely so, obtuse or mucronate, lower pair ovate; petioles up to 10mm. Heads (1-)5-12-fld; peduncles up to c. 15cm., rather slender. Fls 10-12mm. Calyx-teeth spreading in bud, 2 upper with an acute sinus. Otherwise much the same as L. corniculatus. Fl. 6-8. $2n = 12^*$, 24. Hp.

Native. In damp grassy places. 107, H40, S. Throughout the British Is., except the extreme north, but less common than L. corniculatus. Europe from Spain and the northern Balkans to S. Scandinavia and C. Russia; Asia; N. Africa."

Adopting L. pedunculatus in preference to L. uliginosus, presumably on the principle of priority, indicates how close Tutin felt Cavanilles's (1793) description and Schkuhr's (1796) description to be. This point had been considered earlier by Willkomm in 1893 (Page 37) but had not been followed up by other authors until this point.

The result of this re-introduction of L. pedunculatus into the classification in the early 1960's, is clearly shown in the published work at this time. This is so not only in Britain, but also in North America and Australasia.

In 1956 Curtis in 'The Student's Flora of Tasmania'

recognised L. corniculatus, L. tenuis and L. uliginosus, whereas by 1972 Willis in 'A Handbook of Plants in Victoria' refers to L. corniculatus and L. pedunculatus.

He states:

"L. corniculatus L. Spec. Plant. 2: 775 (1753).

Stem + decumbent, solid or nearly so;
leaflets 3-10mm. long, obovate, obtuse;
calyx-teeth erect in bud; pod 2-3cm. long;
W.A., Tas., N.S.W., A.C.T., Qd, N.Z.

L. pedunculatus Cav. Icon. et Descr. Plant.
2: 52, t. 164 (1793).

L. uliginosus Schkuhr Bot. Handb. 2: 412, t. 211
(1796).

Stem erect or ascending, hollow; leaflets
mostly 15-20mm. long, obovate (often obliquely
so), obtuse; calyx-teeth spreading in the bud;
pod 2-3cm. long;
W.A., Tas., N.Z."

Most taxonomists in Europe, however, remained of the opinion that L. pedunculatus and L. uliginosus were two different plants, and that the name L. pedunculatus should be reserved for a plant found locally in Spain around the areas first described by Cavanilles.

Many European authors, such as Mullenders (1967) in 'Flore de la Belgique, du Nord de la France et des Régions Voisines' fail to mention L. pedunculatus at all. Similarly no reference is made to L. pedunculatus as either a separate species or as a synonym for L. uliginosus in the Italian publication 'La Nostra Flora' by Fenaroli (1969).

It is possibly as a result of the work of Ball in collaboration with Chrtková-Žertová to compile the classification in 'Flora Europaea', 1969, in which is pointed out a number of morphological differences between L. pedunculatus and L. uliginosus

that the name L. uliginosus has found favour in Britain again.

In this classification found in 'Flora Europaea', Ball lists 14 species within the L. corniculatus group of which 5 are included below.

"L. tenuis Waldst. & Kit. ex Willd., Enum. Pl. Hort. Berol. 797 (1809) (L. tenuifolius (L.) Reichenb., non Burm. fil.). Stems 20-90cm, glabrous or sparsely pubescent. Leaflets 5-15 x 1-4mm, linear or linear-lanceolate. Heads 1- to 4(-6)-flowered. Calyx-teeth equal, usually shorter than tube; corolla 6-12mm, yellow; wings obovate-oblong. Legume 15-30 x 2-2.5mm. $2n = 12$. Most of Europe except the north-east and extreme north. Al.

L. corniculatus L., Sp. Pl. 775 (1753) (incl. L. ambiguus Besser ex Sprengel, L. caucasicus Kuprian). Stems 5-35cm, procumbent or ascending, glabrous to villous. Leaflets 4-18 x 1-10mm, lanceolate or oblanceolate to suborbicular. Heads (1-)2- to 7-flowered; pedicels 1-2.5mm. Calyx-teeth equal, shorter or slightly longer than the tube, triangular to filiform with triangular base; corolla 10-16mm, usually yellow. Legume 15-30 x 2-2.5mm. $2n = 24$. Almost throughout Europe. All except Sb; introduced in Is.

As described here this species is very variable. It may eventually be possible to recognise a number of subspecies, but the native distribution of this and some related species is very confused, owing to their widespread use as a forage crop.

The main variants which occur in Europe are as follows:

- (i) sparsely to densely pubescent; calyx-teeth shorter than tube (N. part of the range of the species, locally in the south);
- (ii) glabrous or sparsely pubescent; leaflets small, fleshy; calyx-teeth about $\frac{1}{2}$ as long as tube (coasts of W. & N. Europe);
- (iii) villous or densely pubescent; calyx-teeth slightly longer than tube (C. & S. Europe).

Dwarf plants resembling 8 (L. alpinus) in many characters also occur in the mountains.

L. alpinus (DC.) Schleicher ex Ramond, Mem. Mus. Hist. Nat. (Paris) 13: 275 (1825). Like L. corniculatus but stems usually not more than 10cm; leaflets 2-6 x 1.5-4mm; heads 1- to 3(-5)-flowered; corolla 12-18mm. $2n = 12$. Pyrenees, Alps, ? Balkan peninsula.

L. uliginosus Schkuhr, Handb. 2: 412 (1796) (L. pedunculatus auct., non Cav., L. corniculatus subsp. major auct. pro parte). Stems 30-100cm, erect or ascending, subglabrous to villous, hollow. Leaflets 8-25 x 3-15mm, obovate, obtuse, often mucronate, glaucous beneath. Heads 5- to 12(-15)-flowered; pedicels 1-2mm. Calyx-teeth about as long as tube, the upper pair separated by an acute sinus in bud; corolla 10-18mm. Legume 15-35 x 2-2.5mm. $2n = 12$. Marshes and wet grassland. W., C. & S. Europe, extending northwards to 60° N. in Fennoscandia and eastwards to c. 25° E. in Ukraine; often occurring as a casual elsewhere in Europe.

L. pedunculatus Cav., Icon. Descr. 2: 52 (1793). Like L. uliginosus but leaflets rhombic, acute; heads 3- to 8(-10)-flowered; calyx-teeth longer than tube, the upper 2 separated by an obtuse sinus in bud. Stems 40-120cm, pubescent; leaflets 15-35 x 5-12mm; legume 15-40 x 2-3mm. W. & C. Spain, E.C. Portugal."

The classification shows that the main criterion used for distinguishing between L. pedunculatus and L. uliginosus is the angle between the upper two calyx teeth. It is doubtful, however, that this character is uniform, so that to some extent the distinctions that have been drawn are simply an attempt to treat the variation that exists within the group consistently.

Importantly, though for uncertain reasons, the name L. pedunculatus has persisted in Australia, New Zealand and North America, although almost certainly it is the same plant as L. uliginosus. Scoggan (1978) in 'Flora of Canada' makes the following observation, noting its spread since 1894, although it was not recognised in all floras of that time (Page 42).

"L. pedunculatus Cav.

Eurasian; apparently known in N. America only from moist waste places and old fields in Canada, as in s B.C. (L. ulig. reported by Eastham 1947, as introd. as a forage crop and apparently well established along roadside ditches at New Westminster and vicinity; collection from near Hatzie in V), Sask. (Boivin 1966b), s Ont. (near Hamilton, Wentworth Co.; Montgomery 1957), E. Que. (W Gaspé Pen.), N.B. (near St. Stephen, Charlotte Co., where taken by Pickett in 1894; CAN), and N.S. (Boivin 1966b). [L. uliginosus Schk.]."

Recent European work has generally tended to extend the classification to include L. alpinus, a very prostrate form of L. corniculatus. Hess, Landolt & Hirzel (1970) in 'Flora der Schweiz' state:

"*Lotus alpinus* (DC.) Schleicher, *Alpen-Schotenklee*

5-10 cm hoch. Stengel niederliegend, am Ende aufsteigend, meist kahl. Teilblätter bis 0.8 cm. 1-1½ mal so lang wie breit, + kahl oder am Rande bewimpert. Blütenstände 1-3 blutig 6-7 mm lang, fast kahl; Kelchzipfel mit 0.5-1 mm langen Haaren bewimpert, vor dem Aufblühen zusammenneigend. Krone 12-18 mm lang, nach dem Verblühen orange; Schiffchenspitzen purpurn. - Blüte: Sommer. $2n = 12$.

Standort. Alpin, seltener subalpin, Lockere, kalkhaltige und kalkarme, steinige Boden. Schutthalden Weiden, Rasen."

"Alpine podded clover.

5-10cm high. Stem prostrate, turning up at the end, usually glabrous. Leaflets about 0.8cm, 1 to 1½ times as long as broad, more or less glabrous or ciliate at the margins. Peduncle 1 to 3 flowered, 6-7mm long, almost glabrous, calyx teeth with 0.5 to 1mm long hairs, and straight in bud. Corolla 12-18mm long, becoming orange on withering; Keel purple. Flowers in summer.

$2n = 12$.

Localities, Alpine, rarely sub-alpine, loose calcareous and non-calcareous stony soils, screes, meadows and pastures."

In 'Flora Italica', Zangheri (1976) describes L. alpinus as:

"*Pia. alta* + 3-10 cm, alpestre, glabra o + pelosa; capolini a 1-3 fi. (di r. più); fg. in gen. di non più di 8 mm di lung.; cor. lung. 12-18 mm, rossigna all'esterno, specialmente all'apice; radice grossa, legnosa, e pia. assai cespugliosa [2n = 12] -

L. alpinus (DC.) Schleicher ex Ramond."

"Plant height about 3-10cm, alpine, glabrous or more or less hairy, heads of 1 to 3 flowers (seldom more); leaflets in general of not more than 8mm long; corolla 12-18mm long, reddish on outside especially towards tips, root large and woody and plant very much tufted. [2n = 12]."

In Britain, the present situation, as described by Clapham, Tutin and Warburg (1983) in the third edition of 'Excursion Flora of the British Isles' is as follows:

"1. *L. corniculatus* L. Birdsfoot-trefoil. Eggs-and-Bacon

10-40 cm. usually glabrous and spreading. Stolons 0; stem solid or nearly so. Lflets 3-10 mm, lanceolate or oblanceolate to suborbicular, obtuse or apiculate, the lower pair broadly ovate or lanceolate; petioles short. Heads (1-)2-6(-8)-fld. Fls c. 15 mm. yellow, often streaked or tipped with red. Calyx-teeth triangular, erect in bud, the 2 upper with an obtuse sinus between them. Pod up to 3 cm. Fl. 6-9. Generally distributed in grassy places.

2. *L. tenuis* Waldst. & Kit. ex Willd. Slender Birds-foot trefoil

Like 1 but stems more slender, often taller (to 90 cm), much more wiry; lflets linear-lanceolate, acuminate, or rarely narrowly obovate; heads rarely more than 4-fld; fls c. 10 mm; calyx-teeth narrow. Fl. 6-8. In dry grassy places; much less common than *L. corniculatus* and absent from much of the north.

3. *L. uliginosus* Schkuhr. Large Birdsfoot-trefoil

Like 1 but stoloniferous; stems hollow, soft, up to 1 m; lflets 15-20 mm obovate, obtuse or mucronate; heads 5-12-fld; calyx-teeth spreading in bud, the 2 upper with an acute sinus between them. Fl. 6-8. In damp grassy places; widely distributed northwards to Orkney."

Tutin has made two main changes to his 1962 description. L. corniculatus is referred to as 'spreading' whereas previously he had used the word 'decumbent'. From this could be inferred that a wider range of growth habits now occurs in Britain. Secondly, the name 'L. pedunculatus' has been replaced by 'L. uliginosus'. Presumably this indicates the resolution of the L. uliginosus-pedunculatus nomenclature problem. Rose (1981), however, still retains the name L. pedunculatus in his classification.

The numerous problems involved in the division of L. corniculatus sensu lato have been pointed out many times by many botanists. Ball (1968) in 'Flora Europaea' states that,

"The data available at the present are insufficient to produce a comprehensive account of the group, and it is likely that some of the species recognised here are heterogeneous, while others may not be distinct species."

Other taxonomists have subdivided the complex into a large number of species, sub species and varieties, which differ only very little from each other, while some have preferred to form more comprehensive groups so recognising fewer, polymorphic species.

Some distinction of species has been made on the basis of chromosome numbers. L. corniculatus sensu stricto is generally regarded as tetraploid ($2n = 24$). However Zeven and de Wet (1982) state that Landolt (1970) and Somarov & Grant (1971) have found both diploid and tetraploid L. corniculatus. They have suggested that the diploid is a hybrid and the tetraploid is an allotetraploid of L. alpinus ($2n = 12$) and L. pilosus ($2n = 12$).

Chrtková-Žertová (1973), in her monographic study confirms that L. corniculatus is tetraploid ($2n = 24$) and recognises the probability of hybridisation within the species complex. On the other hand she states the likelihood of hybridisation between L. corniculatus and a related diploid species such as L. alpinus to be questionable. Despite this, high altitude forms of L. corniculatus often appear indistinguishable from L. alpinus. The difficulties of separating these species morphologically may have contributed to reports of L. alpinus existing in both diploid and tetraploid forms.

However, Reynaud (1980) states that he was able to recognise L. alpinus growing within populations of L. corniculatus sensu stricto in the Alps. He goes on to say that L. alpinus may be diploid ($2n = 12$) or tetraploid or even hexaploid and that distribution is influenced by altitude and soil type. Diploids are more commonly found between 2200m and 3000m on acidic soils, whereas the upper limit for tetraploids is about 2400m, though they may be found upto 2700m on calcareous soils.

Chrtková-Žertová (1973), comments that L. corniculatus var. alpicola ($2n = 24$) is morphologically similar to L. alpinus ($2n = 12$) and that in a study of var. alpicola in the Carpathian mountains the number $2n = 24$ was established. She states that in this study L. alpinus was not found, it occurring only in the Alps. This disagrees with findings by Borsos (1966) who had earlier reported the existence of L. alpinus in the Carpathian area.

L. tenuis and L. uliginosus are generally regarded as diploid ($2n = 12$). However autotetraploid cultivars of L. uliginosus (L. pedunculatus), such as Grasslands Maku, have been produced in

New Zealand. Although these plants show increased vigour, they are morphologically very similar to the diploid L. uliginosus.

A hexaploid ($2n = 36$) form of L. corniculatus has been reported from the Apennines (Beuret, 1977) and work is also proceeding in New Zealand on the production of allohexaploid crosses between L. corniculatus and L. uliginosus (Charlton pers. comm.). Such developments prompt discussion on the importance of differences in chromosome number when defining species.

Generally a species is characterised by a single chromosome number, which then may serve as a useful taxonomic character. In fact the species concept sees a species as a distinct population where closely related species are kept separate by reproductive isolating mechanisms. These mechanisms prevent or reduce gene exchange. Since plants with different chromosome numbers are usually effectively genetically isolated, for even if hybridisation takes place the progeny are likely to be sterile, then it is claimed there is a case for supporting the view of one species - one chromosome number. Löve & Löve (1974) have expressed and extended this viewpoint to include the notion that differences in chromosome base-number should not be tolerated within a single genus. By using these strict criteria many new genera would be created and species divided when morphological studies alone would have shown no basis for separation, as would be the case with Lotus. Stace (1980) states:

"It is true that the great majority of species separated largely on cytological evidence were earlier recognised as taxonomic entities on morphological grounds, but the differences are often very slight and had often led to recognition at only the infraspecific level. The

redefinition of genera and species by
means of chromosome number alone cannot
be justified."

5.

Materials and Methods

Plants corresponding to the description of Lotus corniculatus sensu lato were collected from a number of sites within the British Isles and Continental Europe. On examination of this material, and also plants which were grown from seed, it became apparent that while L. uliginosus could in most, but not all cases be distinguished immediately from L. corniculatus sensu stricto, there were two forms of the latter species which could also be readily distinguished. The distinction between these two forms was eventually taken to be:

- a) Decumbent form. Plants with stems lying on the soil surface and with none ascending.
- b) Erect form. Plants with any or all of the stems ascending or erect.

On the basis that single characters, especially in an aggregate species as variable as Lotus corniculatus, are of relatively little value in determining the status of different forms, other characters were studied in relation to these two forms to establish whether a case could be made for giving them taxonomic status. Measurements from each of these forms have therefore been separated and the validity for this separation is discussed. In addition, herbarium material from the Royal Botanic Garden, Edinburgh, was examined.

Seeds identified as L. corniculatus, L. uliginosus, L. pedunculatus and L. tenuis were obtained from various sources in Northern, Central and Southern Europe as well as from Canada, the United States and New Zealand.

British Material

Between April and August 1982 material identified as either L. corniculatus or L. uliginosus was collected from 67 sites throughout Britain (Appendix 1) and brought back to the West of Scotland Agricultural College, Auchincruive. Plants and seeds were grown in 4 inch pots in John Innes No. 2 compost. Stems were trimmed back as necessary to a few centimetres above soil level and the plants overwintered in a heated glasshouse. In April 1983, after a hardening-off period, plants were put 1m apart into plots and maintained under more or less uniform conditions. Various morphological measurements of L. corniculatus and L. uliginosus were taken in situ at a further 43 sites and 35 sites respectively, throughout the country.

Continental European Material

Seed was obtained from various sources throughout Continental Europe (Appendix 2). Where seeds were known to have originated from local wild populations the sites of these have been indicated, as have the origins of a small number of whole plants brought from Norway and alpine areas of Switzerland, France and Italy.

The European cultivars grown were: Tarborsky, Puławska, Orsegi, Bursztyn, Odenwälder, Franco, Porto and Hoki.

Canadian, United States and New Zealand Material

North American cultivars grown from seed were: Granger, Morshansk, Mansfield, Wallace, Leo, Maitland, Marshfield, Fargo,

Douglas, Border, Empire, Tana, Westriver, Viking. The New Zealand cultivars grown were Grasslands Maku and a number of unnamed varieties presently undergoing agronomic trials.

Seed was sown between February and December 1982. Seedlings were grown on in John Innes No. 2 compost in a heated glasshouse and after hardening-off in coldframes in the spring were transplanted into the plots along with the British and European material in April 1983.

Following their establishment and growth the Lotus population in the plots comprised 141 plants consisting of 59 L. uliginosus, 41 L. corniculatus (erect form), 34 L. corniculatus (decumbent form) and 7 L. tenuis.

During July and August 1983 morphological measurements were made of each plant using criteria which have previously been employed to distinguish the different species.

Measurements

Leaflet length

5 terminal leaflets from each plant were measured from the leaf tip along the main vein to the leaf base. Where plants were heterophyllous leaflets were taken from the mid-stem region.

Leaflet length:breadth ratio

Breadth was measured across the mid-point of the same leaflets.

Leaflet hairiness

The presence or absence of leaflet hairs was noted. Hairy

forms were classified as either sparsely or densely hairy.

Stem length

The lengths of 3 main stems from each plant were measured.

Hollowness of stems

Cross-sections from 3 main stems from each plant were examined and classified as either hollow with little or no pith, or solid and completely filled with medullary tissue.

Peduncle length

The lengths of 5 peduncles from each plant were measured.

Number of flowers per inflorescence

The number of flowers on 3 inflorescences of each plant were counted.

Seed size

As the length to breadth ratio appeared constant at 1.25, seed length only was taken as an indication of seed size. The lengths of 10 seeds from 20 L. corniculatus (decumbent form), 20 L. corniculatus (erect form), 20 L. uliginosus and 7 L. tenuis taken at random were measured using a haemocytometer.

Calyx teeth : appearance in bud

The calyx teeth of each plant were examined while in bud and categorised as being either spreading or erect (Plates 4 & 5).

Calyx teeth : shape

The calyx teeth were examined when the plants were in full flower and their shape subjectively assessed as being either narrowly pointed or broadly triangular (Plates 6 & 7).

Calyx teeth : angle between two upper teeth

The angle between the two upper calyx teeth was recorded as obtuse if the sinus was rounded or blunt and acute if it was brought sharply to a point.

Length of internodes

The number and length of internodes on 3 main stems of 10 randomly selected plants representing each group were recorded.

Prominence of leaf veins

The undersurface of 3 leaflets from each plant was examined to determine the prominence of the veins. Veins were recorded as being either present or absent. If veins were discernible but not conspicuously present they were classified as distinct.

Leaf epidermal cells

Epidermal tissue, obtained from a leaf tear, was microscopically examined for variation in cell shape and size.

Leaf shape after transplanting

23 L. corniculatus (decumbent form) and 15 L. uliginosus remained alive one year after transplantation from the wild. The

leaflet length and leaflet length:breadth ratio of these plants were compared to corresponding measurements made on the same plants one year previously when growing in wild conditions.

Presence of rhizomes

Plants were examined for the presence of rhizomes. Any rhizomes were themselves examined for the presence of adventitious roots.

Chromosome numbers

Stem cuttings from each plant were grown in a rooting medium of 3 parts sand : 1 part peat in a mist propagator. On establishment, young actively growing roots were removed for root squash preparations and the following procedure was carried out.

The roots were pretreated by soaking in 0.002M 8-hydroxy-quinoline for 1 hour and then fixed in 3:1 mixture absolute alcohol : glacial acetic acid for 24 hours and placed in a refrigerator. On removal they were soaked in 5N hydrochloric acid for 10 minutes and washed in distilled water for 2 minutes. The root tips were excised and stained with lactopropionic orcein. A squash was prepared by repeatedly tapping the material on a glass slide with the tip of a brass rod held vertically. Subsequently the root cells were examined microscopically for variation in chromosome number.

6.

Results

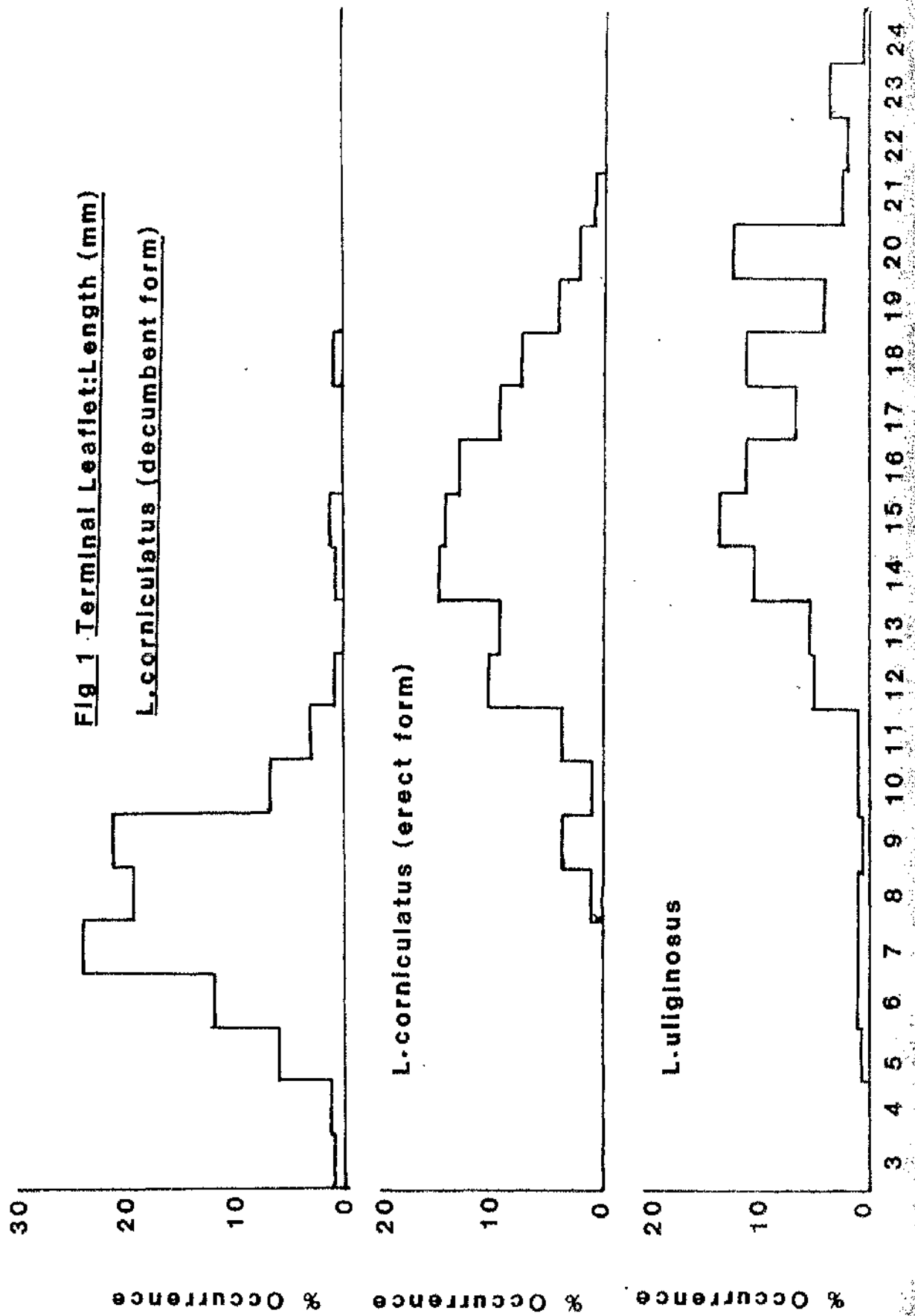
Most of the material studied had been supplied or identified as L. corniculatus or L. uliginosus and as explained previously, L. corniculatus plants were divided into erect and decumbent forms. These three types were the only types available in sufficient numbers for meaningful statistical analyses to be made of the measurements taken. Therefore most of the results deal with the differences between them. However, mention of L. tenuis has been made in cases where it seemed a clear-cut difference existed.

6.1 Leaflet Length

The range over which leaflets vary in length is shown in Fig. 1. Noticeably few plants have leaflets of 10 or 11mm long so that some discontinuity is apparent. Leaflets of 7 to 9mm long are most frequently encountered in the decumbent form of L. corniculatus, whereas in the erect form leaflets of 12 to 17mm are most common. Occasional plants of decumbent L. corniculatus were found with long leaves.

The range of leaflet length in L. uliginosus overlaps considerably with that of the erect form of L. corniculatus although a small percentage of the population may be found with leaves longer than any in the erect L. corniculatus population.

No significant differences (Table 2) are found between L. uliginosus and the erect form of L. corniculatus with respect to leaflet length. However both of these populations are



significantly different from the decumbent form of L. corniculatus.

Table 2: Mean Leaflet Length (mm)

	Mean length	Standard Deviation (S.D.)	Standard Error (S.E.)
<u>L. uliginosus</u>	16.5	4.0	0.23
<u>L. corniculatus</u> erect form	14.5	3.1	0.22
<u>L. corniculatus</u> decumbent form	7.8	2.1	0.16

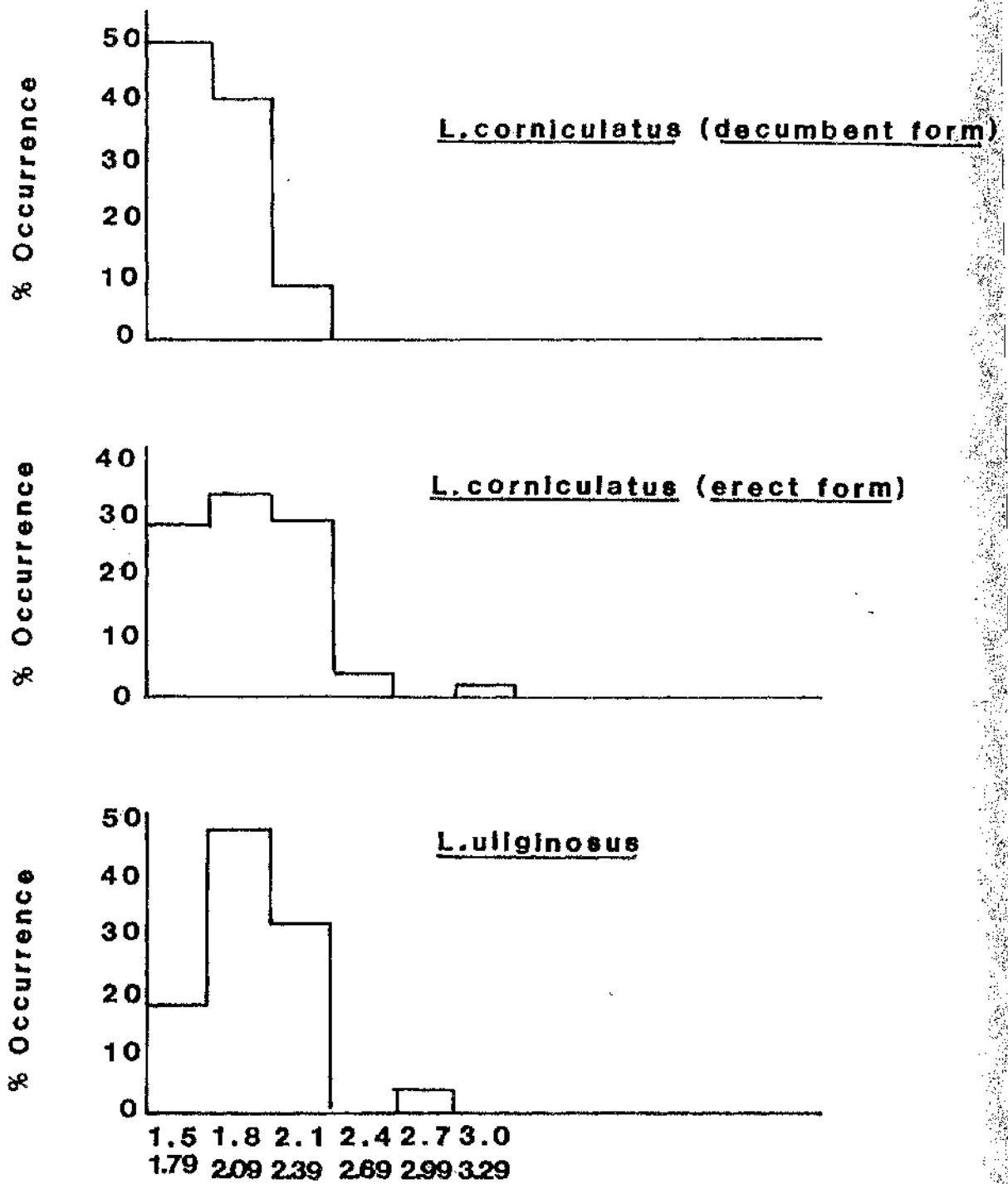
6.2 Leaflet Length to Breadth Ratio

Fig. 2 shows that the leaves of L. uliginosus and the erect form of L. corniculatus are most frequently obovate and slightly more than twice as long as broad. There appears to be no significant difference (Table 3) in this ratio between these two species. However both these length to breadth ratios are significantly different from that found in the decumbent form of L. corniculatus. In this population most frequently the leaves are less than twice as long as broad so the leaves appear broader and more rounded than in either the erect form of L. corniculatus or L. uliginosus. L. tenuis has significantly longer and thinner leaves than the others.

Table 3. Mean Leaflet Length to Breadth Ratio

	Mean ratio	S.D.	S.E.
<u>L. uliginosus</u>	2.03	0.26	0.03
<u>L. corniculatus</u> erect form	2.10	0.56	0.09
<u>L. corniculatus</u> decumbent form	1.83	0.24	0.02
<u>L. tenuis</u>	3.1	0.28	0.04

Fig 2 Terminal leaflet:Ratio of Length to Breadth



6.3 Leaflet Hairiness

Hairs, when present, generally appear short and weak and occur on both stems and leaves. Some plants may appear hairy on some stems but glabrous on others.

Fig. 3 shows that hairs may be found on plants of both species though more so on L. uliginosus than either form of L. corniculatus.

L. uliginosus is mostly sparsely hairy with 13% of the population densely so. The decumbent form of L. corniculatus is also commonly hairy with a greater proportion being densely hairy. Least frequently hairy is the erect form of L. corniculatus with only 7% of the population being densely so. A significant proportion of all three types is glabrous.

6.4 Stem Length

Fig. 4 and Table 4 illustrate the significant discontinuity in the range of variation in stem length of L. corniculatus. Stems of the decumbent form rarely exceed 200mm, whereas stems in the erect form are rarely less than 250mm.

Stem length in L. uliginosus is more variable than L. corniculatus but with the majority of the population extending over the same range as that of the erect form of L. corniculatus, no significant difference is apparent.

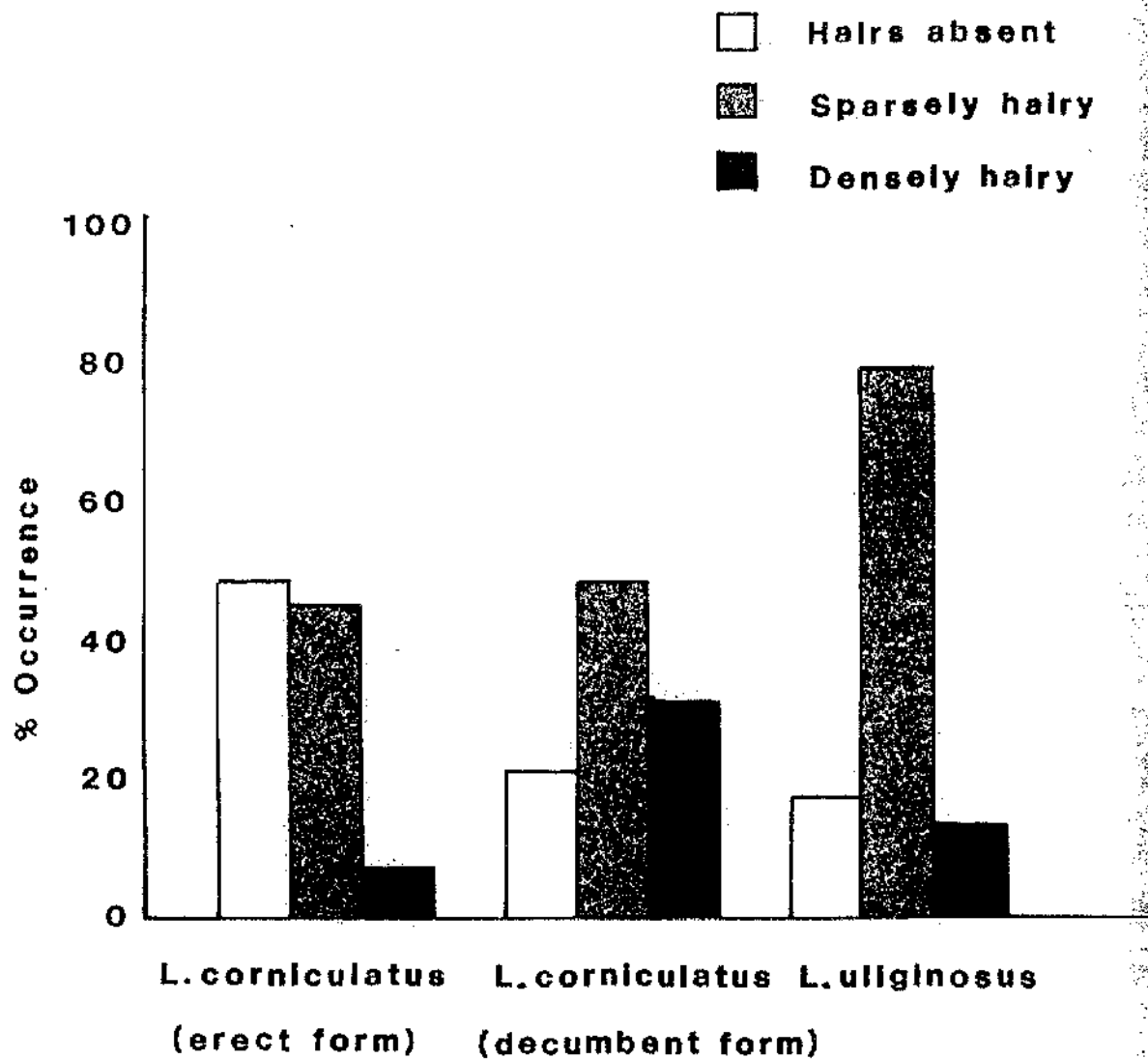


Fig 3 Leaflet Hairiness

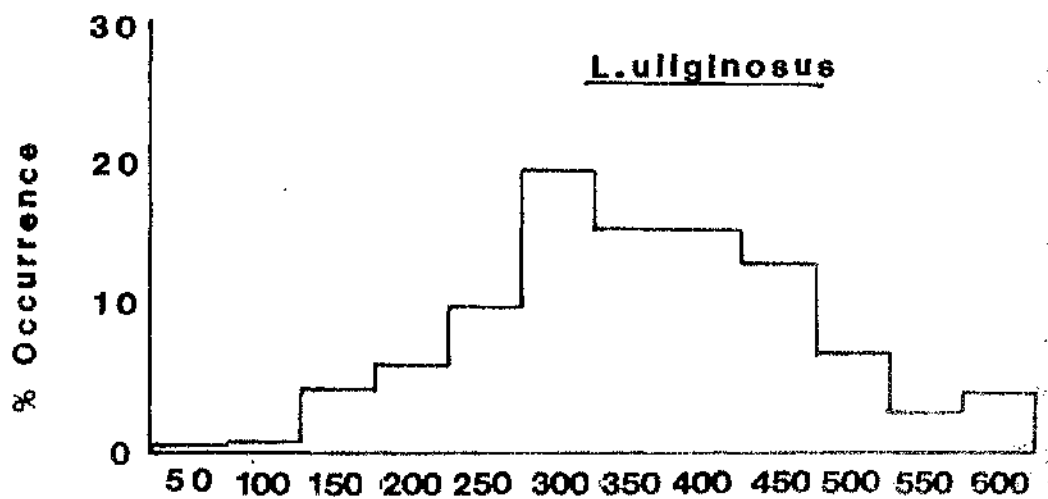
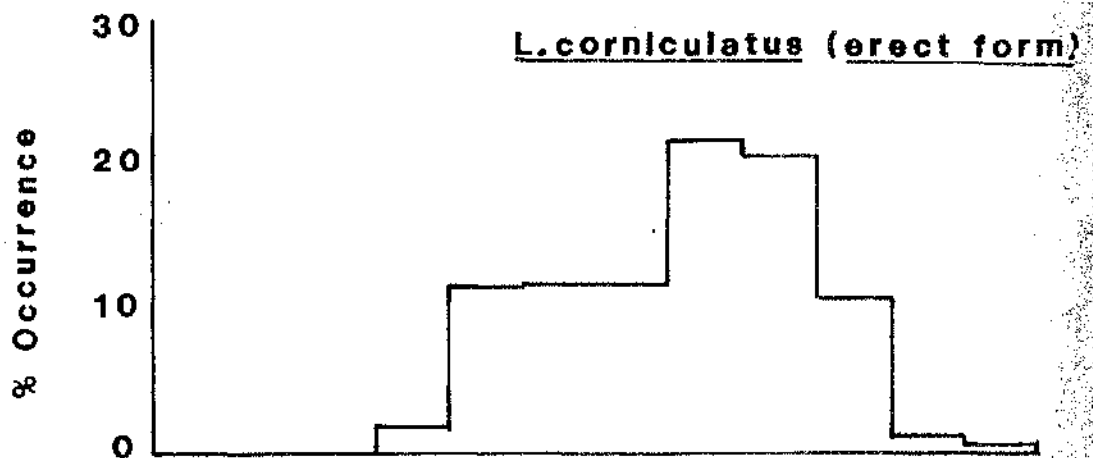
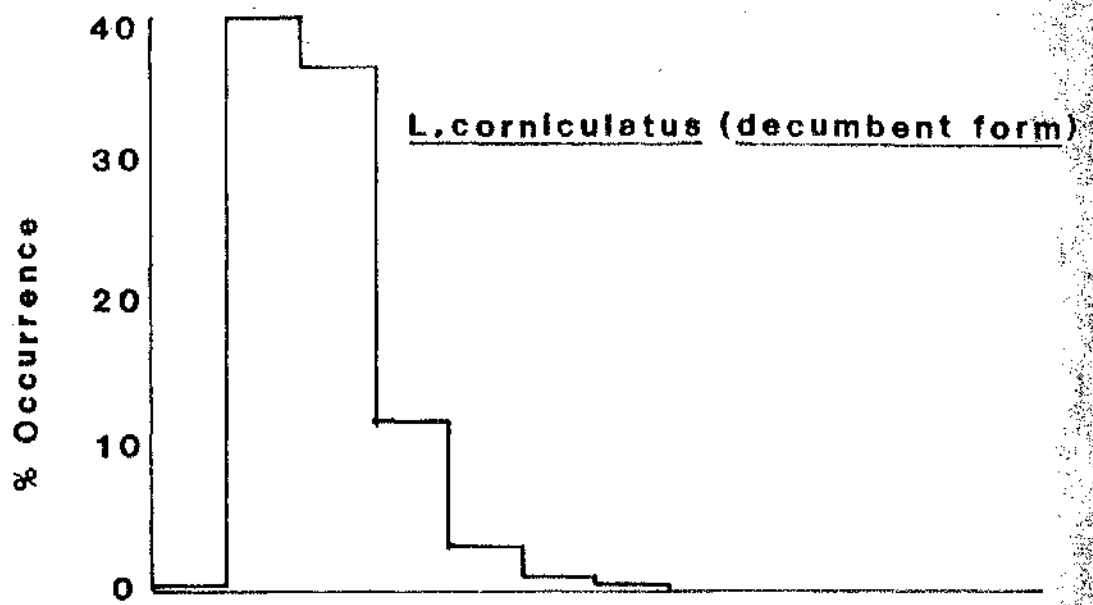


Fig 4 Stem Length (mm)

Table 4: Mean Stem Length (mm)

	Mean length	S.D.	S.E.
<u>L. uliginosus</u>	356	112	8.5
<u>L. corniculatus</u> erect form	385	90	7.7
<u>L. corniculatus</u> decumbent form	146	53	5.0

6.5 Hollowness of Stems

Fig. 5 shows that the large majority of plants in the L. uliginosus population have hollow stems, whereas almost all of the decumbent forms of L. corniculatus have solid stems. While the majority of the stems of the erect form of L. corniculatus are also solid at the base, in this group of the plants this character is seen more to be intermediate between L. uliginosus and the decumbent form of L. corniculatus.

6.6 Peduncle Length

Fig. 6 shows that there is considerable overlap in peduncle length between the two forms of L. corniculatus. Because of this, peduncles on the decumbent form may sometimes appear proportionately longer than on the erect form when related to stem length.

In L. uliginosus the variation in peduncle length is considerable (Table 5) and peduncles upto 30mm longer than the longest found in the erect form of L. corniculatus were observed.

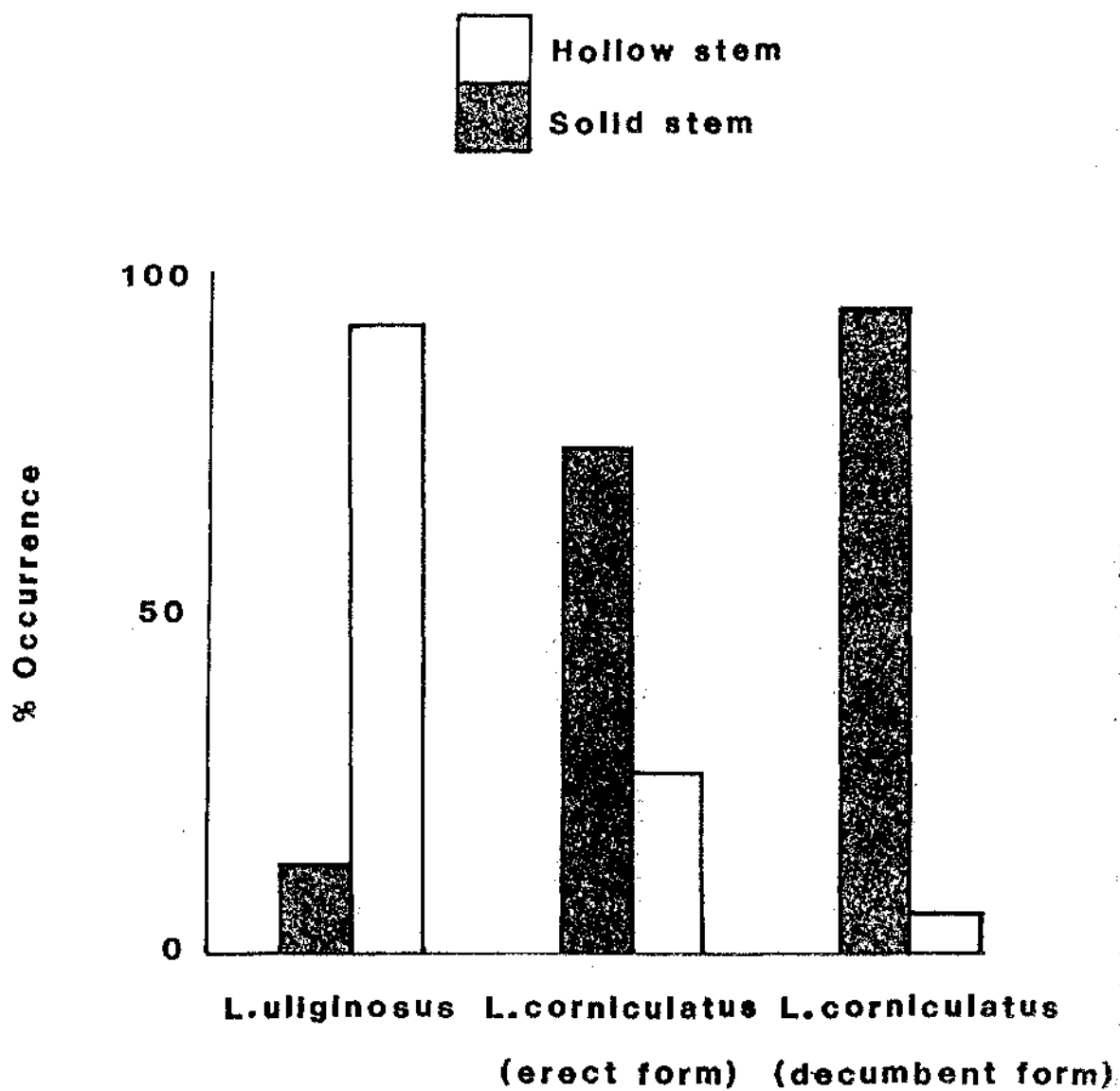


Fig 5 Hollowness of Stems

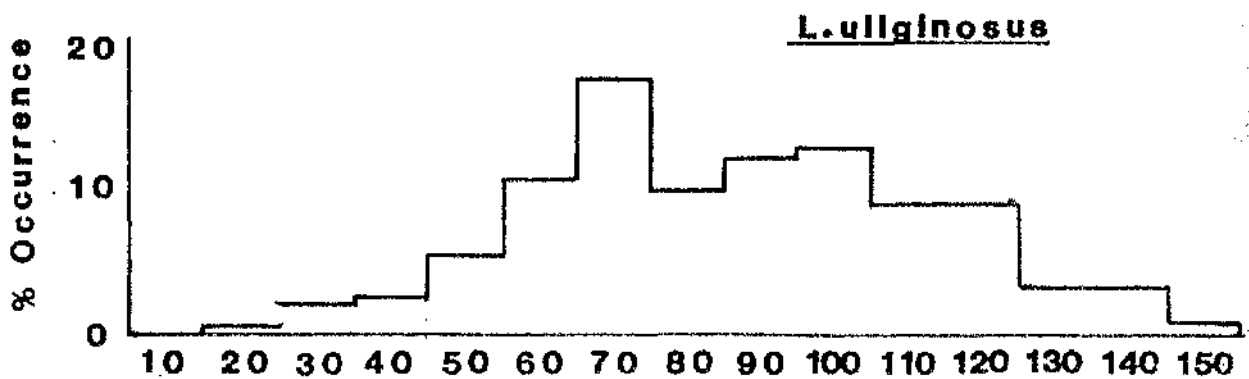
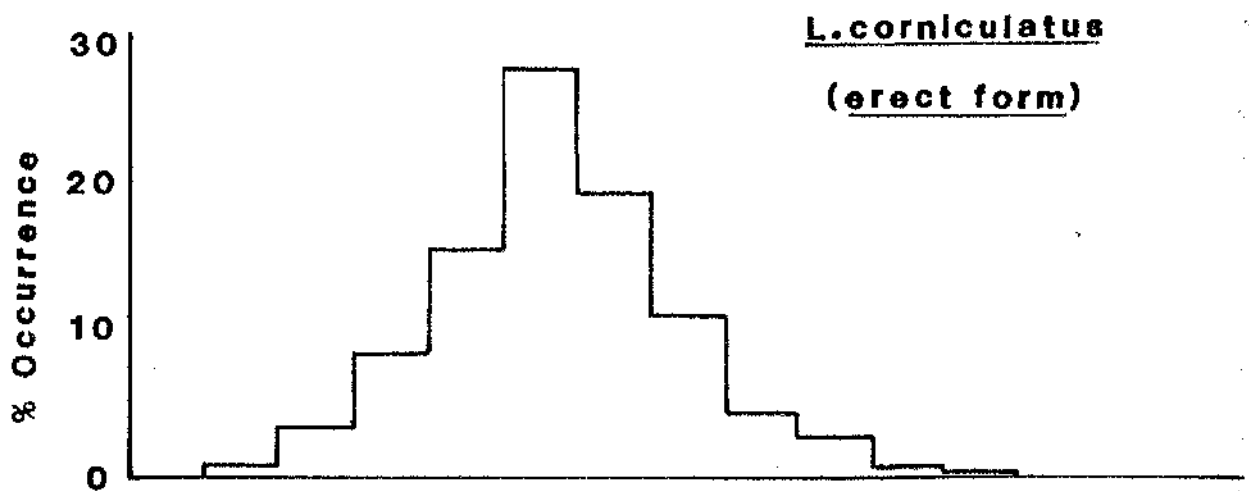
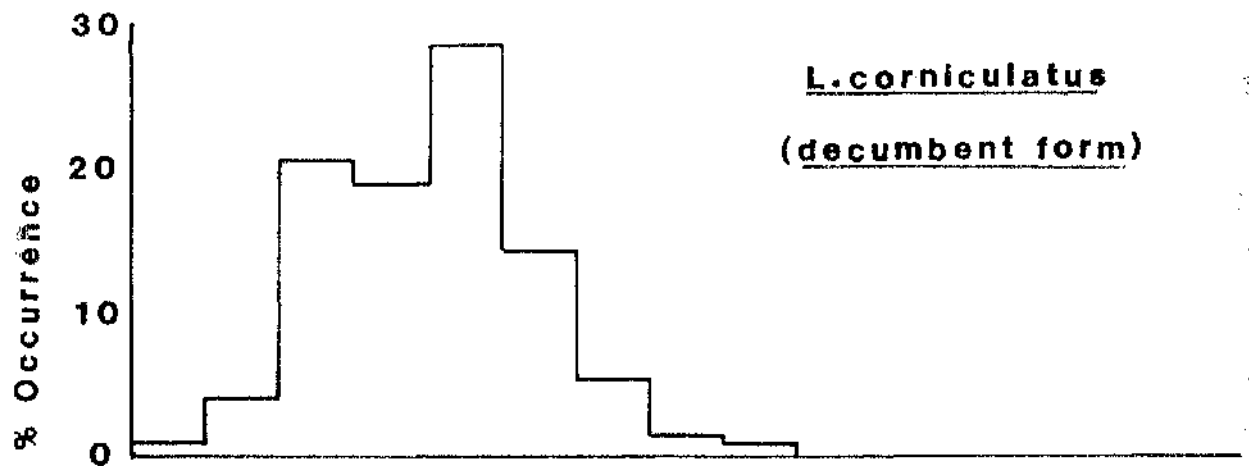


Fig 6 Peduncle Length (mm)

Table 5: Mean Peduncle Length (mm)

	Mean length	S.D.	S.E.
<u>L. uliginosus</u>	85.7	26.3	1.6
<u>L. corniculatus</u> erect form	63.3	17.4	1.2
<u>L. corniculatus</u> decumbent form	44.7	16.2	1.3

6.7 Number of Flowers per Inflorescence

Fig. 7 shows that the number of flowers per inflorescence in L. corniculatus ranges from 1 to 8. However, the decumbent form is commonly found with 3 to 5 flowers per inflorescence whereas the erect form more frequently has 5 to 7 flowers. Thus the variation found in each form appears to be part of the same normal distribution for this character.

L. uliginosus is again much more variable and although it is found with 4 to 15 flowers per inflorescence it is most commonly found with 5 to 12.

The differences among the three populations are significant (Table 6).

Table 6: Mean Number of Flowers per Inflorescence

	Mean number	S.D.	S.E.
<u>L. uliginosus</u>	9	2	0.18
<u>L. corniculatus</u> erect form	6	1	0.08
<u>L. corniculatus</u> decumbent form	4	1	0.09

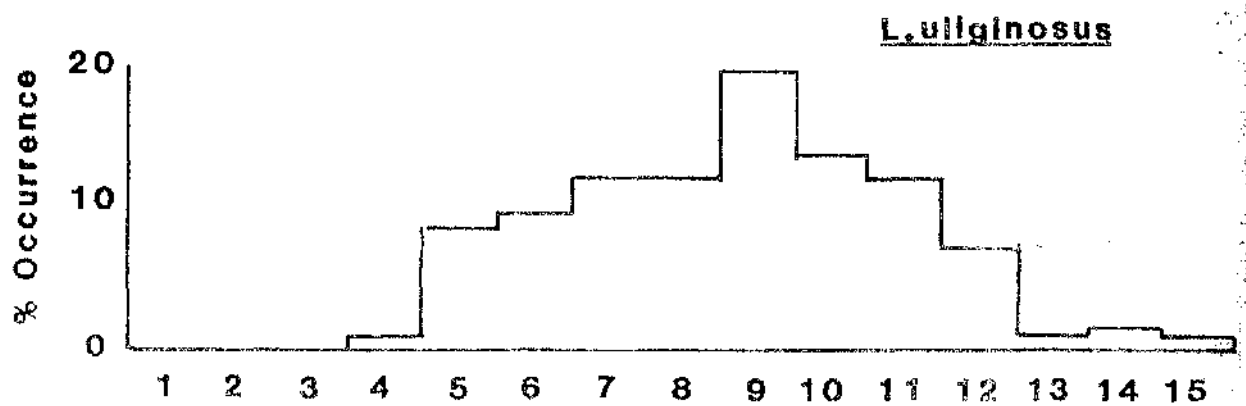
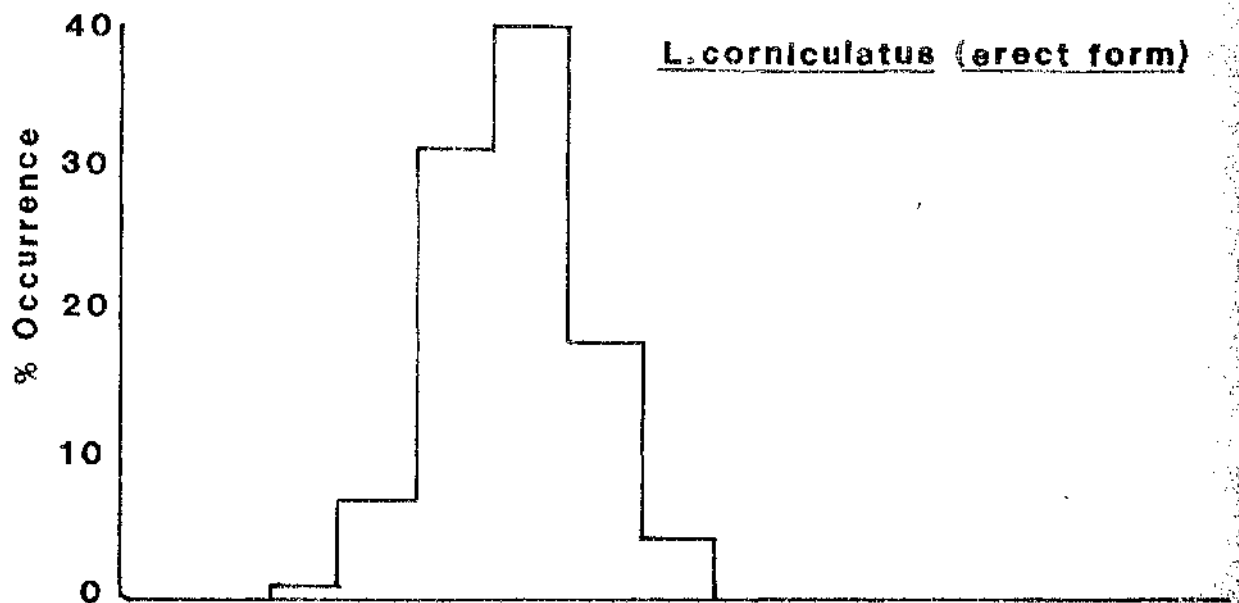
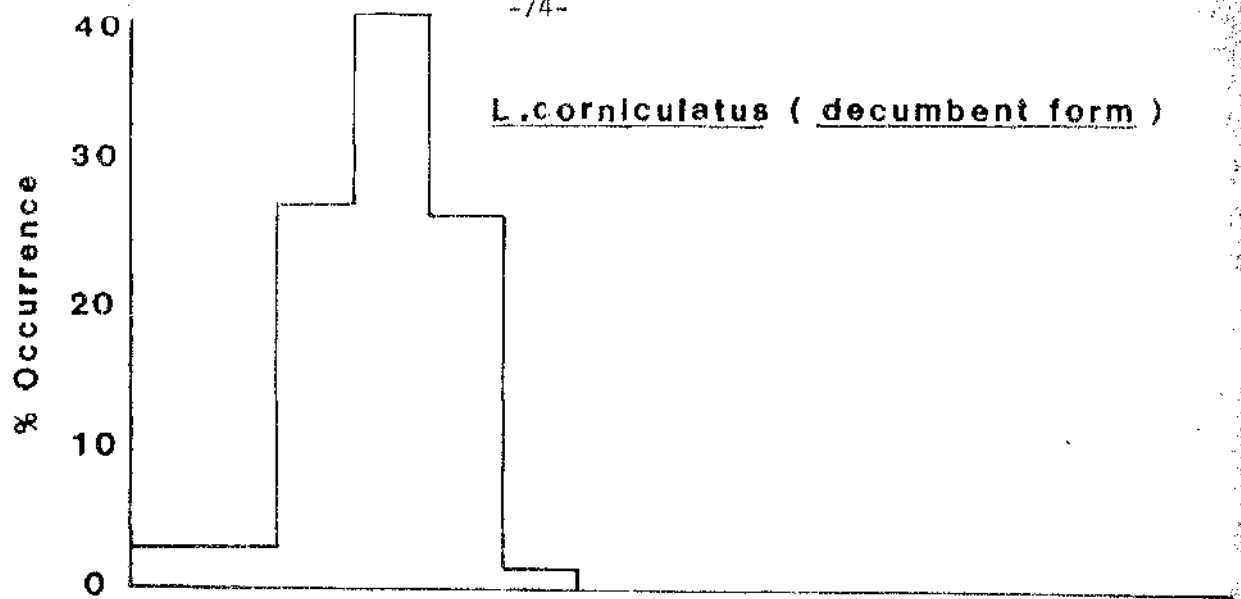


Fig 7 Number of flowers/Inflorescence

6.8 Seed Length

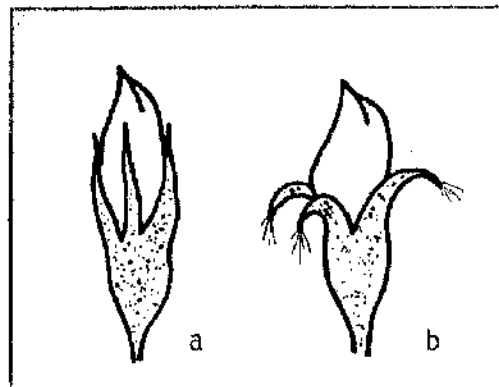
Fig. 8 shows that no distinction on seed length can be made between the two forms of L. corniculatus. In both cases seeds varied from the smallest at 0.76mm to the largest at 1.66mm.

Seed of L. uliginosus is significantly smaller and is most frequently 0.76 to 0.88mm long, although the range extends from 0.5 to 1.14mm.

Seed of L. tenuis is indistinguishable in size and range from L. corniculatus.

6.9 Calyx Teeth in Bud

Plates 4 and 5 illustrate the calyx teeth of L. uliginosus and L. corniculatus when in bud. In all cases the calyx teeth of L. uliginosus were seen to be spreading whereas in L. corniculatus, decumbent and erect forms and L. tenuis, the calyx teeth were straight or erect. Erect calyx teeth are shown in (a) below and can be seen to continue in the same line. Spreading calyx teeth are bent back at right angles to the calyx tube (see b below).



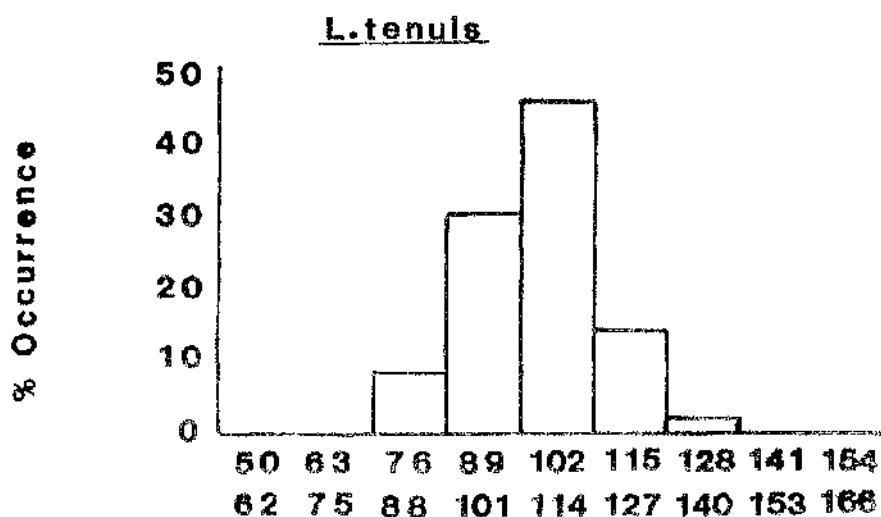
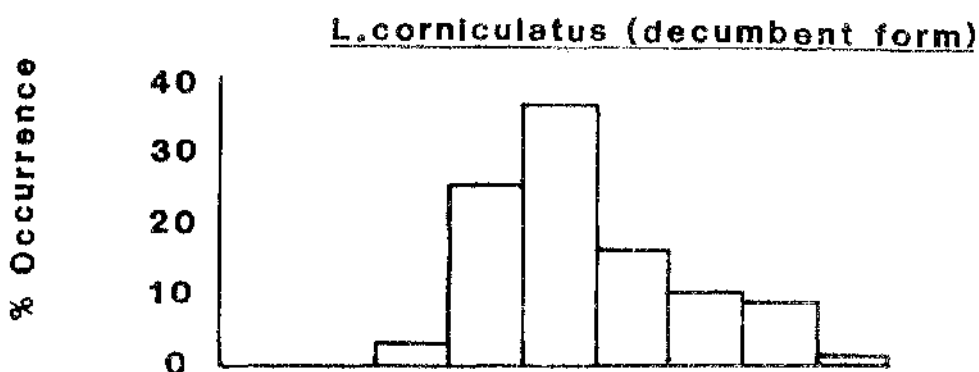
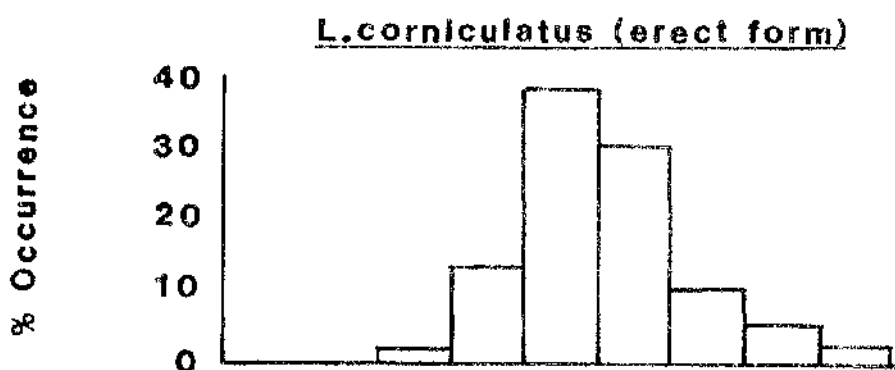
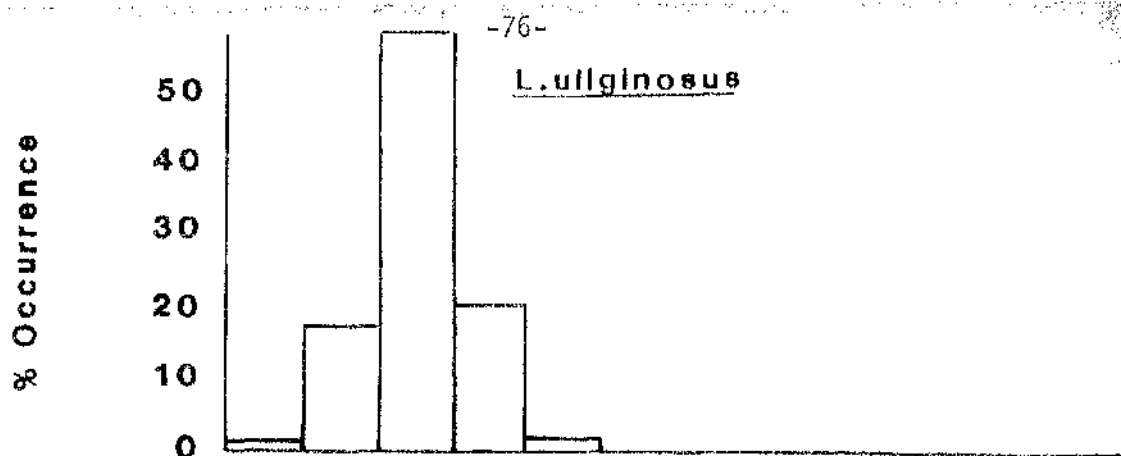


Fig 8 Seed Length (mm^{-1})



Plate 4 L.uliginosus : calyx teeth in bud



Plate 5 L.corniculatus : calyx teeth in bud

6.10 Angle between upper two Calyx Teeth

In the majority of cases the angle between the upper two calyx teeth of both species was acute. It was obtuse in 4% of the L. uliginosus population, 9% of the erect L. corniculatus and not at all in decumbent L. corniculatus population. The angle could vary markedly however, even in the same inflorescence.

Plate 6 shows an inflorescence of L. corniculatus viewed from above with the standard petals trimmed to reveal the calyx teeth and the angle between them. The various angles occurring in the same inflorescence can be seen. Thus depending upon the flower selected, the angle between the upper two calyx teeth, of this particular plant, could be described as acute, intermediate or obtuse. Such inconsistencies were observed also in L. uliginosus.

6.11 Length of Calyx Teeth

Plate 7 shows an inflorescence of L. corniculatus viewed from above with two of the standard petals trimmed to reveal the longer calyx teeth. The variation that exists in length and shape of the teeth even within a single inflorescence may be seen. Thus within one population long, narrowly pointed teeth may be found as well as short and broadly triangular teeth.

Similar inconsistencies were also observed in the L. uliginosus population.

Table 7, overleaf, shows that most frequently calyx teeth are found to be narrowly pointed, and that both species occur with broadly triangular teeth, particularly the decumbent form of L. corniculatus.

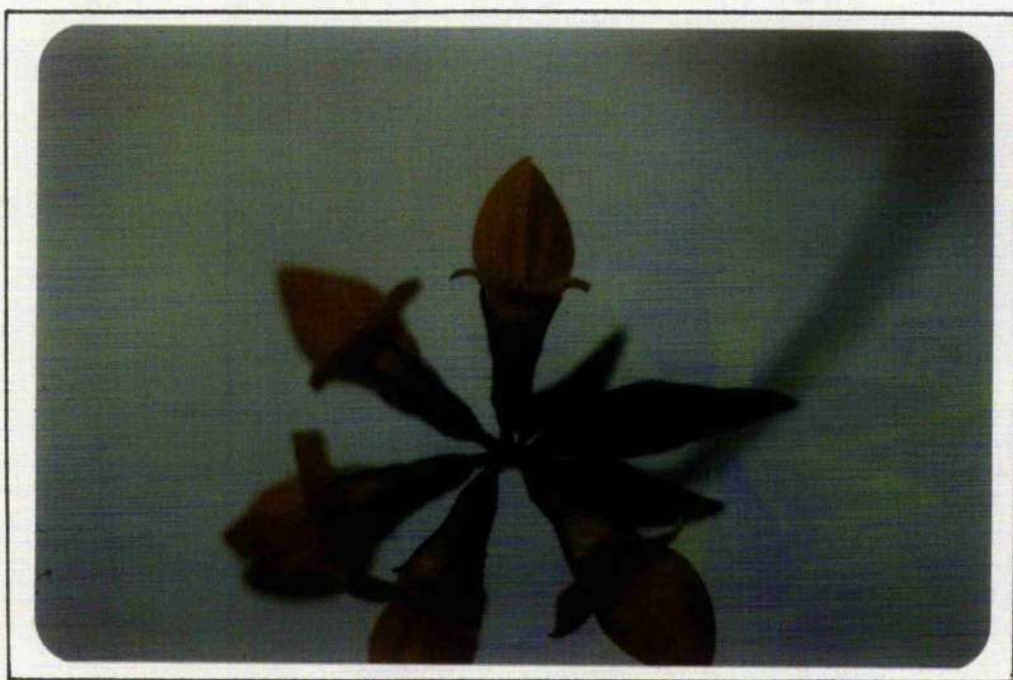


Plate 6 L.corniculatus : angle between calyx teeth



Plate 7 L.corniculatus : length of calyx teeth

Table 7: Shape of Calyx Teeth

	Percentage of inflorescences occurring with calyx teeth		
	Narrowly Pointed	Broadly Triangular	Both
<u>L. uliginosus</u>	73	13	14
<u>L. corniculatus</u> erect form	88	8	4
<u>L. corniculatus</u> decumbent form	52	33	15

6.12 Length of Internodes

L. uliginosus is very variable in its appearance with the erect form of L. corniculatus slightly less so. No significant difference was observed between the internode lengths of these two plants. The decumbent form of L. corniculatus however, is much less variable having more and shorter internodes so that the larger number of secondary stems give the plants a bushier and significantly different appearance. Plates 8, 9, 10 and 11 show the growth habit of plants representative of each population and Table 8 indicates the differences in internode length.

Table 8: Mean Internode Length (mm)

	Mean length	Average number per plant	S.D. of internode length	S.E. of internode length
<u>L. uliginosus</u>	24.8	12.4	16.9	1.53
<u>L. corniculatus</u> erect form	27.5	10.8	10.0	0.95
<u>L. corniculatus</u> decumbent form	9.3	16.0	4.5	0.38



Plate 8 L.corniculatus (decumbent form)



Plate 9 L.corniculatus (erect form)



Plate 10 L.uliginosus



Plate 11 L.tenuis

6.13 Prominence of Leaf Veins

Table 9 shows that in L. uliginosus leaf veins are generally distinctly visible on the undersurface of the leaves. In contrast the leaf veins of the decumbent form of L. corniculatus are generally absent. This character is more variable in the erect form of L. corniculatus where in half the population leaf veins were absent, and present in varying degrees in the other half.

Table 9: The prominence of leaf veins

	Percentage of plants occurring with leaf veins		
	Absent	Indistinct	Distinct
<u>L. uliginosus</u>	2	18	80
<u>L. corniculatus</u> erect form	50	29	21
<u>L. corniculatus</u> decumbent form	82	18	0

6.14 Leaf Epidermal Cells

Plates 12 and 13 show examples of leaf epidermal cells in L. corniculatus and L. uliginosus. Differences in shape are apparent but the range of variation was considerable, both in these two species and in L. tenuis. It was found impossible to distinguish these species by this character.

6.15 Leaf Shape after Transplantation

Tables 10 and 11 show that significant changes take place in



Plate 12 **Leaf epidermal cells of L.corniculatus**



Plate 13 **Leaf epidermal cells of L.uliginosus**

leaflet length and leaflet length to breadth ratio in the L. uliginosus and L. corniculatus (decumbent form) population one year after transplantation.

In cultivation leaflets show an increase in length of between 20 to 40%. They also increase in breadth by 60 to 70%. This affects not only the overall size of the leaflets but also their shape so that they become less lanceolate and more broadly ovate or obovate.

Table 10: L. uliginosus: Leaf Shape after Transplanting

	Terminal leaflets			Length to breadth ratio		
	Mean length (mm)	S.D.	S.E.	Ratio	S.D.	S.E.
In wild	12.7	4.0	0.62	2.7	0.7	0.24
In cultivation	15.5	3.9	0.61	2.0	0.2	0.06

Table 11: L. corniculatus (decumbent form): Leaf Shape after Transplanting

	Terminal leaflets			Length to breadth ratio		
	Mean length (mm)	S.D.	S.E.	Ratio	S.D.	S.E.
In wild	5.4	2.2	0.20	2.1	0.4	0.08
In cultivation	7.7	1.6	0.14	1.8	0.2	0.05

6.16 Presence of Rhizomes

All plants were examined for the presence of rhizomes. In most cases these were found to be absent in L. corniculatus. However in some, stems ran horizontally below the ground for a few centimetres. These were white or cream in colour but no adventitious roots were found. The only exception to this was seen in prostrate Norwegian material possibly L. corniculatus var. norvegicus where weak adventitious roots were discovered in plants grown in pots. This material only became available late in the work and no observations were possible on its growth in the field. In contrast rhizomes were found to be present in most L. uliginosus plants. These often rebranched forming an underground system with strong adventitious roots. The tips of these rhizomes were frequently found upturned and lying on the surface of the ground.

6.17 Chromosome Numbers

Plates 14 and 15 show metaphase preparations of the chromosomes of L. uliginosus and L. corniculatus at approximately 3000x magnification. In all L. uliginosus and all L. tenuis material examined, the number of chromosomes $2n = 12$ was recognised, whereas in all L. corniculatus the number $2n = 24$ was established.



Plate 14 Chromosomes of L. uliginosus

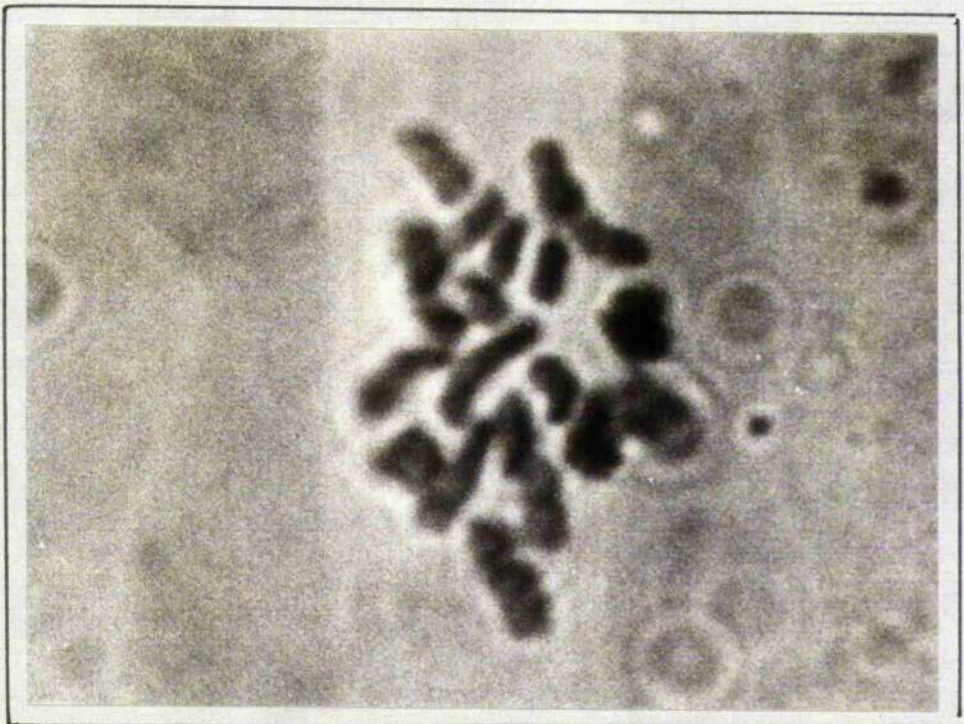


Plate 15 Chromosomes of L. corniculatus

7.

Discussion

Lotus corniculatus s.l. is not a group of species whose taxonomy may be defined precisely by genetic or morphological limits. Rather, its wide ecological range, widespread geographic distribution and polymorphous nature contrive to make the position more complex. Few characters show breaks in variation to enable relatively distinct categories to be recognised. This is not unusual. There are many species or groups of species where the same situation occurs. Stace (1980) recognises that the existence of these polymorphous complexes precludes precise definition. However, he does suggest four criteria, of which one or more may be applied, to help distinguish species.

- "1. The individuals should bear a close relationship to one another such that they are always readily recognizable as members of that group.
2. There are gaps between the spectra of variation exhibited by related species; if there are no such gaps then there is a case for amalgamating the taxa as a single species.
3. Each species occupies a definable geographical area (wide or narrow) and is demonstrably suited to the environmental conditions which it encounters.
4. In sexual taxa, the individuals should be capable of interbreeding with little or no loss of fertility, and there should be some reduction in the level of success (measured in terms of hybrid fertility) of crossing with other species."

As none of these criteria is absolute, it must be recognised that the category of a species is a flexible unit of practical convenience.

In trying to produce a workable classification, most

taxonomists look for discontinuities in variation to establish boundaries. With such a widespread and variable group as L. corniculatus s.l., it is not surprising that it has been separated into a number of taxa, very different in size and degrees of diversity c.f. Koch (1843) and Hegi (1907).

The range of species now recognised in 'Flora Europaea' is considerable. Ball (1968), in describing the group, lists 14 species of L. corniculatus and distinguishes them by their perennial character from the annuals L. angustissimus L., L. subbiflorus Lang. and L. parviflorus Desf. The validity of such a distinction may be questionable. Whyte (1977) has discussed the relationship between perennial and annual growth habit in the genus. He indicates that further work could be carried out to establish which perennial species show degrees of annuality, and to what extent. This may be particularly important along the boundaries of their natural range where physiological stress may affect the situation. However, knowledge of the ecological habitats of some of the minor species and sub-species and their distribution is limited. O'Brien (1974) states that,

"there is incomplete collection over the geographic range giving incomplete range of characters within the recognisable groupings. Collections have been concentrated in the geographic area around herbaria or from known "good collecting localities". A few good specimens are considered sufficient."

This view is substantiated by the difficulty experienced in obtaining local minor species listed in 'Flora Europaea'. It is also cause to question the identity of material which apparently exists in herbaria only. This study examines three of the more easily available species (of British importance): L. corniculatus s.s.,

L. tenuis and L. uliginosus.

On initial examination of L. corniculatus, it was apparent that the stems varied from decumbent to erect and that the difference in appearance between the two extremes was very great. A number of intermediate ascending stages also existed. However, similarities in other morphological characters including leaflet length, stem length, internode length and number of flowers per inflorescence clearly indicated that these intermediate forms were more closely associated with the erect rather than the decumbent form. This enabled a useful general statement to be made distinguishing two groups of L. corniculatus according to growth habit; one group having all stems decumbent, and the other group having any or all stems ascending or erect.

There is a precedent for such a definition, for it is apparent from early descriptions (Linnaeus (1753)) that L. corniculatus was thought of as a decumbent plant. Linnaeus' diagnosis is "*Lotus capitalis depressis, caulibus decumbentibus, leguminibus cylindricis*". Lotus with heads flattened from above, decumbent stems, cylindrical pods. Early botanists, von Haller (1742), Scopoli (1772), Gray (1821) and de Candolle (1824-74) all agree on this point. Schkuhr (1796), does not describe L. corniculatus but makes reference to a decumbent plant he calls L. arvensis.

Linnaeus (1753) recognised the erect forms, L. rectus and L. hirsutus. These he distinguished on pubescence, L. hirsutus being hairy and L. rectus being glabrous. There must be doubt, however, as to the reliability of this character for separation of

plants at a specific level (Fig. 3).

Scopoli (1772) used the name L. major to describe an erect plant and later Cavanilles (1793) introduced L. pedunculatus, including an illustration of the plant (Plate 3) in 'Icones et Descriptiones Plantarum'. This clearly shows the calyx teeth of L. pedunculatus, in common with those of L. corniculatus, to be erect in bud. When Schkuhr (1796) described another erect form, L. uliginosus, he too found the character of calyx teeth useful. While in bud the calyx teeth, according to Schkuhr, are bent back in L. uliginosus so distinguishing it from L. corniculatus. This particular character made identification relatively easy when the plant was in bud. At other stages of growth distinguishing L. uliginosus from erect forms such as L. pedunculatus remained difficult if not impossible for many workers. This inevitably led to taxonomic confusion. Descriptions given by Clapham, Tutin and Warburg (1952, 1962 and 1983) show how opinion in Britain has varied. In 1952 the plant was named L. uliginosus. In 1962 this was changed to L. pedunculatus and in 1983 Tutin reverted to L. uliginosus.

Opinions on this matter are still divided and a dichotomy in the usage of the name L. pedunculatus appears to have arisen. In Europe the name is used to describe a locally occurring species of L. corniculatus in Southern Spain, whereas in Australasia and North America it is regarded as synonymous with L. uliginosus. Forde (1974) discusses this issue and states,

"The confusion cannot easily be resolved, because it is permissible to take a broad or a narrow view of species limits in this group. In the broad view, L. pedunculatus Cav. sensu lato is the

correct name for the entire pedunculatus-uliginosus group, including the cultivated forms. In the narrow view, L. pedunculatus Cav. sensu stricto can be used only for the species described by Cavanilles from the mountains of Spain (present distribution outside Spain and Portugal unknown), in which case L. uliginosus Schkuhr is the correct name for the widespread form(s). Where no qualification is given it is not clear in what sense the name is being used."

Others, Chrtková-Žertová (1966) and Lainz (1974) consider the two species distinct. They describe L. uliginosus as a European species with a sub-atlantic range, distributed throughout the greater part of Europe and in North-West Africa. L. pedunculatus, however, is reported as a west-Mediterranean endemic species with a range limited to Eastern and Southern Spain.

Ball (1968) regards the two species as similar though distinguishable by a number of morphological features. He considers L. uliginosus to have obovate leaflets with the upper two calyx teeth separated by an acute sinus. By contrast he finds that L. pedunculatus has rhombic leaflets and an obtuse sinus in bud. Both of these characters, however, have been shown to be unreliable (Page 50). The attitude of the calyx teeth in bud might have been a more useful distinguishing feature. This was not described.

Historically, several morphological characters have been used to separate erect forms of L. corniculatus from L. uliginosus, though few can claim to show the necessary discontinuity of variation to allow certain identification. The weight of evidence obtained from several characters, however, may provide sufficient information for identification in the field.

Leaf shape is one such frequently used character, despite the occurrence of a range of different shapes, even on the same plant. The erect form of L. corniculatus is frequently heterophyllous. While it is useful to identify L. tenuis on the basis of its linear or linear-lanceolate leaves, such a character appears to be of little value for distinguishing between erect forms of L. corniculatus and L. uliginosus. Leaflets may be linear, ovate, obovate or rhombic and considerable overlap exists at both inter-specific and intra-specific levels. It has been shown, however, that the decumbent form of L. corniculatus frequently occurs with more uniformly broader and shorter leaflets than other forms (Page 65).

Hairiness, as previously mentioned, is also of doubtful value. Although L. uliginosus is frequently found to have leaflets fringed with hairs, similar numbers of L. uliginosus and erect L. corniculatus were found to be glabrous. As long ago as the 17th century, Gerard (1633) may have referred to the degree of hairiness of the horned clover when describing its leaves as "white". A similar description was later provided by Linnaeus (1753) in 'Species Plantarum', "*Lotus polyceratas frutescens incana alba*" where the woolliness of the hairs gave an impression of whiteness (Page 9).

L. corniculatus continued to be separated into varieties according to hairiness. Koch (1843) describes the glabrous var vulgaris and the densely hairy var hirsutus. It is now known that pubescence may be environmentally induced and that differences may occur during ageing (Chrtková-Žertová, 1973). Even at an

intra-specific level, hairiness is an unreliable criterion for separation, particularly in some varieties of prostrate L. corniculatus such as var crassifolius which possesses both glabrous and hairy forms.

Various other characters appear to be of greater value. Most classifications have described the number of flowers per inflorescence for each species. Clapham, Tutin and Warburg (1983) state that L. corniculatus frequently has from 2-6 flowers whereas L. uliginosus has 5-12 flowers per inflorescence. Earlier, Babington (1843) found L. corniculatus to have 5-10 flowers and L. uliginosus to have 8-12 flowers per head. Earlier still, Gray (1821) described L. corniculatus as having from 8 - 10 flowers whereas L. uliginosus he accredited with the unusually large number of 20 flowers per head.

The results show that the decumbent form of L. corniculatus was not found to occur with more than 6 flowers per head and the erect form with no more than 8 flowers per head. L. uliginosus, however, most frequently has 9 flowers though the exact number may vary between 4 and 15. While erect forms with fewer than 8 flowers per head would therefore be of no value for identification purposes, such a plant with more than 8 flowers per head would indicate the plant was L. uliginosus.

Another useful but inconclusive feature for identification purposes is the hollowness of stem. Schkuhr (1796) first referred to this feature in L. uliginosus and by contrast noted the solid stems of L. arvensis, a decumbent corniculatus. Since then, most authors have thought this an important character, and the

results show that in the majority of cases L. uliginosus does occur with hollow stems while the reverse is true of decumbent L. corniculatus. Difficulties arise when using this character to distinguish between some large, erect forms of L. corniculatus and L. uliginosus. In the former, while the base may be solid or finely bored the upper parts of the stem may be as tubular as that of L. uliginosus. Of note is Cavanilles' (1793) description of the stem of L. pedunculatus as "fleshy". On this evidence, it would seem that Cavanilles was describing L. corniculatus rather than L. uliginosus with which it has been confused.

A distinction considered important by Brand (1898), but rarely referred to, is the variation in the prominence of leaf veins. Brand found the leaf veins of L. uliginosus to be conspicuous on the undersurface whereas in L. corniculatus they could not be seen. Although this is not a consistent feature, it is apparent that it may be of some value when used with caution. Leaf veins were found to be distinctly prominent in 80% of all L. uliginosus examined and in only 21% of erect forms of L. corniculatus, whereas none was visible in the decumbent form of L. corniculatus.

Possession of stolons or rhizomes has frequently been used to distinguish between L. corniculatus and L. uliginosus. Clapham, Tutin & Warburg (1983) state that L. corniculatus has no stolons whereas L. uliginosus is stoloniferous. Unfortunately the situation is not this clear. Underground stems are not always present in L. uliginosus and yet may be present in decumbent forms of L. corniculatus, particularly in sandy areas. Stolons do not

occur in erect plants. Such stolons or rhizomes are prostrate stems, partly buried at the base and often originating from low on the crown. However no British material identified as L. corniculatus was found to produce adventitious roots along these rhizomes. This was not so of Norwegian L. corniculatus which was observed to have thick rhizomes with small adventitious roots. These, however, were only observed on plants grown in pots (Page 86).

Chrtková-Žertová (1973) states that although absence of underground stems in L. corniculatus has been regarded as a diagnostic character, some varieties characteristically possess them. They occur regularly, especially in var. crassifolius and var. norvegicus.

It is apparent that the morphological features discussed so far fall well short of providing sufficient distinction to enable the construction of a neat classification. However there are some discontinuities in the range of variation which enable relatively distinct categories to be recognised. When in bud, the spreading calyx teeth of L. uliginosus are an immediately recognisable character different from the straight calyx teeth of L. corniculatus or L. tenuis. Moreover the entirely decumbent habit of one form of L. corniculatus distinguishes it from other ascending or erect types. If additional geographical or ecological evidence is also incorporated, as would be desirable, then the situation becomes clearer still. Rarely is L. corniculatus found in persistently wet soils while it is unusual to find L. uliginosus in dry locations, although overlap does occur in intermediate conditions in the West of Scotland (Williams pers. comm.).

It is possible, therefore, on the basis of these findings to suggest descriptions of four groupings of birdsfoot trefoil.

L. corniculatus

a) Erect type. Plants varying in form from having some, but not all, stems decumbent to ascending or erect. Stems (20) 25-50 (60) cm, usually solid at base but frequently becoming hollow. Internodes long 15-38cm. Peduncles (2) 3-10 (13) cm. Leaves glabrous or hairy, ovate, obovate often mucronate, 8-21mm long, usually more than twice as long as wide, veins usually absent or scarcely apparent. Inflorescence 3-8 flowered. Calyx teeth erect in bud. Underground stems absent. (2n = 24).

b) Decumbent type. Plants with all stems decumbent, low and spreading. Stems (5) 10-25 (35) cm, usually solid. Internodes short 5-13cm. Peduncles erect (1) 2-7 (9) cm. Leaves glabrous or hairy ovate or obovate (3) 5-12 (15) mm long, usually less than half as long as wide, veins usually absent. Inflorescence 1-6 flowered. Calyx teeth erect in bud. Rootstock short and thick, often woody with underground stems, adventitious roots occasionally present. (2n = 24).

L. uliginosus. Plants varying in form with stems procumbent, ascending or erect. Stems (5) 15-50 (60) cm, often branched, usually hollow. Internodes 12-36cm. Peduncles (2) 3-12 (15) cm. Leaves sometimes glabrous but frequently hairy, especially around margins, ovate, obovate or mucronate (5) 12-20 (24) mm long, more than twice as long as wide, veins usually distinct on undersurface.

Inflorescence (3) 5-12 (15) flowered. Calyx teeth spreading in bud. Underground stems well developed bearing adventitious roots. ($2n = 12$).

L. tenuis. Plants varying in form from decumbent to erect. Stems upto 90cm, solid. Internodes long giving stems a bare appearance. Leaves usually glabrous, linear-lanceolate or lanceolate, more than three times as long as wide. Inflorescence (2) 6-8 (9) flowered. Calyx teeth erect in bud. ($2n = 12$).

The justification for awarding L. uliginosus, L. tenuis and L. corniculatus species status is not based solely on distinctions of morphology. An important definition of a species is its ability to cross. It is generally conceded that while individuals within a species are capable of interbreeding, the level of success is reduced when crossing with other species. There is considerable experience by plant breeders (Forde pers. comm.) that L. corniculatus, L. uliginosus and L. tenuis will cross only with great difficulty. Induced L. corniculatus x L. uliginosus hybrids are agronomically useful in New Zealand and L. uliginosus x L. tenuis hybrids have been produced for studies of Rhizobium specifically (Greenwood & Ross, 1974). More work on the genetics of the group and aspects such as Rhizobium specificity may provide clearer definitions.

Attempts, however, to split L. corniculatus s.l. into a large number of infra-specific taxa, are of doubtful value. Nevertheless, the taxonomist can point out and discuss the variation. In so doing, if categories can be reasonably defined, then the taxonomist is justified in attaching names to them. In this way, attention is drawn to that taxon. The "International Code of

Botanical Nomenclature" recognises five infra-specific ranks: subspecies, variety, subvariety, form, subform. Present trends encourage the use of only one, that of subspecies. This was defined by Du Rietz (1930) as:

"a population of several biotypes forming a more or less distinct regional facies of a species"

It may thus be regarded as a geographical race or ecotype. However Stace (1980) reports that nowadays the sub-specific rank embraces not only these forms but also physiological races, seasonal variants and various other relatively minor morphs which taxonomists wish to name. A consequence of this, according to Stace, is that this lack of means to express infra-specific variation leads to an over-splitting of a species. As "Flora Europaea" (1964-80) deals only with sub-species below the species level, then many forms may have been recognised as sub-species only because if they had been retained as varieties no mention of them would have been possible. This contraction of the system of classification may in part account for the inclusion of the large number of forms of L. corniculatus at specific level.

If two distinct forms of L. corniculatus (erect and decumbent) are recognisable in Britain, then using the same approach as "Flora Europaea", it may be possible to justify giving each sub-species status. Evidence from the morphological studies would suggest that the erect form could be called ssp. major after Scopoli (1772) and the decumbent form ssp. corniculatus after Linnaeus (1753), according to the rule of priority. However, there are a number of difficulties associated with this nomenclature.

Gray (1821) and Smith (1825) both used L. major as a synonym for L. uliginosus. This view has been supported by a number of taxonomists: Coste (1937), MacDonald (1946), Munz & Keck (1959). To reintroduce the name L. major for this purpose would be to perpetuate one aspect of the taxonomic confusion.

A number of alternatives are available. Chrtková-Žertová (1973) has separated L. corniculatus into 14 infra-specific ranks termed varieties, 4 of which appear close to the British erect form. These are var. corniculatus, var. sativus, var. kochii and var. arenosus, the latter two being specifically hairy forms.

To use the name ssp. corniculatus for an erect form would contradict Linnaeus (1753) who, in his original diagnosis, described L. corniculatus as a decumbent form. The description of var. sativus is precluded from use too. The range of variation it delimits is too narrow to encompass that found in the erect form. Var. sativus is essentially a tall plant with a hollow stem, heads (1) 3-5 (6) flowered, and glabrous or sparsely hairy. These characters do not necessarily correspond to all British material.

Chrtková-Žertová includes no completely decumbent form in her classification, though var. crassifolius has a number of morphological features which fit the British decumbent form. Underground shoots are present, stems are solid, leaf shape and number of flowers per inflorescence correspond. Var. crassifolius does vary strongly according to ecological conditions which particularly affect degree of hairiness. She also states that a distinctive feature of this form is the strongly fleshy leaflets. While this is true of some of the British population, it was not found to be a consistent feature. Chrtková-Žertová's studies of

British material were limited to herbarium specimens only.

Hughes, Heath & Metcalfe (1962) cite MacDonald's (1946) classification based on the work of Hegi (1924) and Robinson (1934). Hughes et al. state

"Two sub-species have been recognised within the broadleaf group (excluding L. tenuis - a narrow leaf trefoil). The erect form common to Continental Europe has been referred to as L. corniculatus var. vulgaris Koch, and the more dwarf form of the British Isles as L. corniculatus var. arvensis Pers."

In view of the difficulties discussed above it would seem that to use 'vulgaris' and 'arvensis' as sub-species epithets would be the most acceptable.

Koch (1843) also describes two other forms of contrasting hairiness, var. ciliatus and var. hirsutus (Page 32). These, it is suggested, should be lumped with ssp. vulgaris to form a more comprehensive group. Problems arising from extensive subdividing, especially on the basis of unreliable characters, are thus avoided. Chrtková-Žertová (1973), in discussing the problem of nomenclature, stated that there is no complete discontinuity among varieties which form part of a "hybridogenous complex", and Heyn (1970) has also commented that "the almost impossible task of the division of the L. corniculatus complex has been pointed out repeatedly." In such cases, once the extent of the variation is noted, it can only be treated informally. This avoids the necessity of naming categories that cannot reasonably be defined.

A further aim of this work was to consider whether any of the features in this group of species could usefully be introduced into cultivars to increase their economic potential. Examination

of existing cultivars or selections of L. corniculatus showed that they all corresponded to sub-species vulgaris in having erect or ascending stems and no rhizomes. While such types can be useful for cattle, grazing must be controlled to prevent excessive defoliation. Sheep too, would probably graze closely enough to destroy the crowns of the plants. As a major requirement of a forage species for less fertile soils, under British conditions, is that it is able to withstand close grazing over which there may only be limited control, it is not surprising that trials with birdsfoot trefoils have shown little long-term potential (Davies, 1969).

New Zealand is one source of commercial seed where their emphasis on introducing L. uliginosus into their breeding programme offers considerable promise. The rhizomatous habit should help withstand sheep grazing, and the greater tolerance of damp conditions should prove useful on some hill and upland farms in western Britain.

For drier areas, other sources of suitable material must be considered, not only from Britain but also North America. In Canada work is being carried out into forage productivity in new cultivars of L. corniculatus (Khayrallah & Lawson, 1976). Their results have indicated that in general, high yield, vigour and winter hardiness are closely associated. There also appears to be a correlation between prostrate growth habit and winter hardiness. While the same may be true of some of the decumbent forms of L. corniculatus in Britain, they have been ignored in breeding programmes, mainly because of their low yields. As some plants are rhizomatous, however, it may well be worthwhile trying to

incorporate this character into a higher yielding type. This might be done more readily than attempting to incorporate genes for rhizomatous habit from L. uliginosus into indigenous L. corniculatus. A number of new sources of material exist, particularly Norwegian L. corniculatus of the type var. norvegicus which has been shown to produce rhizomes bearing adventitious roots, (this has been confirmed in pot-grown plants only).

Leaflet size also plays a part in determining the usefulness of L. corniculatus as a forage crop. Results (85) indicate that L. corniculatus and L. uliginosus show significant increases in both size and shape of leaflets after transplanting from wild to cultivated conditions. Although a taxonomically superficial feature, increased leaflet area, brought about mainly by increased leaflet breadth, has important agronomic implications. Other features also affecting yield and dependent on habitat include size of plants, number of stems and number of leaves per stem (Chrtková-Žertová, 1973).

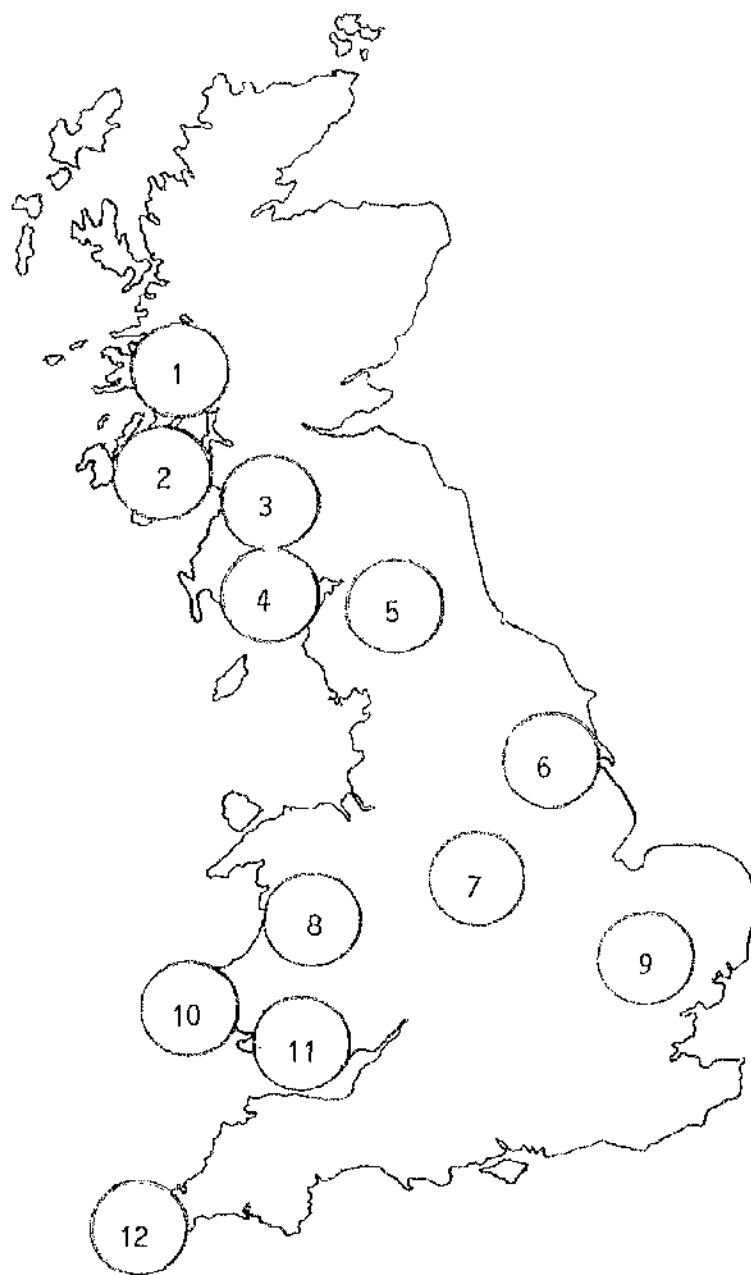
An attempt has been made in this study to survey the great extent of the variability of L. corniculatus s.l. There is no doubt that the genetic potential is present for the development of new varieties suitable for agricultural use in Britain.

Appendix 1

Sources of British Plant Material

Key	Region	Site Grid Reference 1:25,000 O.S. Maps.	<u>L. corniculatus</u>	<u>L. uliginosus</u>
1	Oban	NM 885688		Yes
2	Kintyre	NR 822608	Yes	
		808603	"	
		799595	"	
		788588		"
		787587		"
		740548		"
		737541		"
		718496	"	
		692467	"	
		658320	"	
		656290	"	
		656289	"	
		655278	"	
		675234	"	
		655261	"	
		786308		"
		778576		"
		852680		"
3	Cumbræ	NS 154541	"	
		149546	"	
		149548	"	
		153558	"	
		158566	"	
		168588	"	
		175591	"	
		179593	"	
		181579	"	
		175569	"	
		174569	"	
		173574	"	
		168568	"	
		167567	"	
		173542	"	
	Ayrshire	NS 348276	"	
		339363	"	
		296164	"	
		305140	"	
		385234		"
		324324	"	
		355152		"
		364148		"
		415195		"

Key	Region	Site Grid Reference 1:25,000 O.S. Maps.	<u>L. corniculatus</u>	<u>L. uliginosus</u>
	Carsphairn	NX 570919		Yes
4	Gatehouse	NX 492630 403517	Yes	"
5	Alston	NY 831497	"	
6	Lincolnshire	SE 995469 TA 105216	" "	"
7	Keele	SJ 821452 SJ 771483	" "	
8	Talerddig	SN 935010		"
9	Cambridgeshire	TL 756820 840810 912883	" " "	
10	St. Davids	SM 725290 750295	" "	
11	Porthcawl	SN 110150 SS 790820 SS 800815	"	" " "
12	Lands End	SW 343252 373272 378290 375332 382384 431370 495395 501372 500313	" " " " " " "	" " " "
	Lizard Downs	701140 736205 724167 679249 667269 665280	" " " " " "	



Sources of British Plant Material

Appendix 2

Sources of Continental European Plant Material

	<u>Material Obtained</u>
1. Nigardalen Glacier Jostedalen Indre Sogn Norway.	L. corniculatus from wild
2. Universitets Botaniske Have Ø. Farimagsgade 2B DK-1353 København K Denmark.	L. corniculatus from wild
3. Bereich Botanik der Humboldt- Universität Späthstrasse 80/81 DDR-1195 Berlin-Baumschulenweg German Democratic Republic.	L. corniculatus
4. Botanischer Garten Sektion Biowissenschaften Martin-Luther-Universität Halle-Wittenberg Am Kirchtor 3 DDR-402 Halle German Democratic Republic.	L. corniculatus L. uliginosus from wild
5. Botanischer Garten der Karl-Marx- Universität Linnestrassse 1 DDR-7010 Leipzig German Democratic Republic.	L. corniculatus L. tenuis from wild L. uliginosus
6. Jardin Botanique de la Ville et de l'Université 5 place Blot F-14000 Caen France.	L. corniculatus L. uliginosus from wild
7. Jardin Botanique de la Ville de Rouen 7 rue de Trianon 76100 Rouen France.	L. corniculatus from wild
8. Botanischer Garten der Universität Karlsruhe Am Fasanengarten 2 D-7500 Karlsruhe 1 Federal Republic of Germany.	L. corniculatus

Material Obtained

- | | | |
|---|--|------------------|
| <p>9. Ville de Nantes
Service Espaces Verts et
Environnement
Jardin Botanique
F-44000 Nantes
France.</p> | <p>L. corniculatus
L. tenuis</p> | <p>from wild</p> |
| <p>10. Jardin Botanique
Universite Louis Pasteur
28 rue Goethe
F-67083 Strasbourg Cedex
France.</p> | <p>L. corniculatus
L. uliginosus</p> | <p>from wild</p> |
| <p>11. Jardin Botanique de la Ville
1 avenue Albert-Premier
F-21000 Dijon
France.</p> | <p>L. corniculatus
L. pedunculatus
L. tenuis</p> | <p>from wild</p> |
| <p>12. Jardin Botanique de la Ville et
de l'Université
Place du Marechal Leclerc
F-25000 Besançon
France.</p> | <p>L. corniculatus
L. uliginosus</p> | <p>from wild</p> |
| <p>13. Botanischer Garten der Universität
Bern
Altenbergrain 21
CH-3013 Bern
Switzerland.</p> | <p>L. corniculatus</p> | |
| <p>14. Botanischer Garten
Brauerstr. 69
CH-9016 St Gallen
Switzerland.</p> | <p>L. corniculatus</p> | |
| <p>15. Direction des Conservatoire et
Jardin botaniques
Case postale 60
CH-1292 Chambesey/Genève
Switzerland.</p> | <p>L. corniculatus
L. uliginosus</p> | <p>from wild</p> |
| <p>16. Jardim Botânico da Universidade
Arcos do Jardim
Coimbra
Portugal</p> | <p>L. corniculatus
L. uliginosus</p> | <p>from wild</p> |
| <p>17. Italian/Swiss Alps
Semnoz (1000m-1700m).</p> | <p>L. corniculatus from wild</p> | |
| <p>18. French Alps
Col de Bluffy (630m).</p> | <p>L. corniculatus from wild</p> | |



Sources of Continental Plant Material

Appendix 3

Source of New Zealand Material

Dept. of Scientific and Industrial Research,
Grasslands Division,
Palmerston North,
New Zealand.

L. corniculatus

L. uliginosus

Source of North American Material

Material originating from the United States and Canada was
obtained from Botany Department stocks, West of Scotland
Agricultural College, Ayr.

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